

## Systematics of the indigenous hares of Italy traditionally identified as *Lepus europaeus* Pallas, 1778 (Mammalia: Leporidae)

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**Abstract.** Hares living on the Italian Peninsula and in Sicily have traditionally been identified as a single species (*Lepus europaeus* Pallas, 1778) but a taxonomic study based on the size, morphology, and pelage of indigenous specimens of this area held in museum collections clearly reveals that they belong to two different species, *L. europaeus* and *Lepus corsicanus* de Winton, 1898. The geographic localities of the specimens indicate that they occupied parapatric areas in natural conditions, *L. europaeus* in the northern part of the Italian Peninsula and *L. corsicanus* in the southern part, being separated between Siena and Rome. The two species are very distinct phenetically and the species differentiation is possible using both univariate and multivariate statistics. There is a notable uniformity in the phenetic characteristics of each species within the natural areas of distribution and no evidence of hybridization has been found as the specimens do not have intermediate characters even in neighboring localities within their geographic areas. Among the discriminant features determining the distinctiveness of these two species the color of the basal fringe of the dorsal underfur of adult specimens which is always white in *L. europaeus* and grey in *L. corsicanus* is worthy of note. As for skull size, there are several measurements which do not overlap, *L. corsicanus* being smaller than *L. europaeus*. As regards dental characters, the difference in the shape of the posterior contour of the cross section of the first upper incisor, which is concave in *L. europaeus* and smooth or convex in *L. corsicanus*, is important. Statistical comparisons of frequencies of skull and dental character states showed high Chisquare values and very low probabilities suggesting that there is a significant difference between the two species. Two correspondence factor analyses based on the above frequencies served to separate well the specimens of the two species into different groups without plot overlapping. As regards phenetic relationships of *L. corsicanus* with other SW European hares, *L. castroviejoi* from the Cantabrian Mts showed the most extensive phenetic similarity in a discriminant analysis made with skull measurements, whereas *L. europaeus* was the most distant. The results suggest that *L. corsicanus* and *L. castroviejoi* could have had a common ancestor occupying a large distribution area in SW Europe between Italy and Spain before the expansion of *L. europaeus*.  
**Key words.** Taxonomy, systematics, hares, *Lepus*, Leporidae, Lagomorpha, mammals, Europe.

### Introduction

Unlike in other Mediterranean countries, hare systematics in Italy have never been a controversial topic. Two species were commonly accepted as representing the hares of the Italian peninsula, *Lepus europaeus meridiei* Hilzheimer, 1906, described from Aveyron (S France) and *Lepus corsicanus* de Winton, 1898, described from Corsica. Shortly after the description of the two taxa, Miller (1912) identified both hares as subspecies of *L. europaeus*. According to this author, the northern Italian hares correspond to *L. europaeus meridiei* and the southern Italian hares to *L. europaeus corsicanus*.

Miller's view accepting these hares only as different subspecies seems unusual for a period in which this author and many other taxonomists were very generous in recognizing the validity of hare species, and the decision seems a little incongruent in comparison with other taxonomic interpretations, as in the case of *Lepus parnassius* Miller, 1903 from Greece, in which the holotype has the typical skin and skull of *L. europaeus*. However, in Italy Miller (1912) separated peninsular hares only at the subspecies level despite the fact that he clearly identified *L. europaeus corsicanus* on the basis of peculiarities of pelage color, and even after detecting the discriminant underfur color of *L. corsicanus* in specimens from Sicily and southern Italy.

Petter (1961) in a wide revision of European and Asiatic hares classified both Italian subspecies under *Lepus capensis*, without making any particular reference to the hares from Italy. In a descriptive work on Italian hares, Toschi (1965) followed Miller (1912) and Ellerman & Morrison-Scott (1951) for taxonomy on peninsular and Sicilian populations.

Following these papers nobody has paid further attention to the study of Italian hares and in the latest publications updating the main taxonomic problems still affecting Old World hares by Flux (1983), Angermann (1983), Corbet (1986), and Flux & Angermann (1990) there is no reference to them. However, in a recent review, Hoffmann (1993) lists *L. corsicanus* as a valid species on the basis of a preliminary contribution on this same subject (Palacios et al. 1989).

### Material and methods

I studied hare specimens from Italy held in the collections of the Istituto Nazionale di Biologia della Selvaggina "Alessandro Ghigi" (Bologna), Museo Civico di Storia Naturale (Milan), Museo Civico di Storia Naturale "Giacomo Doria" (Genova), Museo Zoologico de "La Specola" (Florence), Unidad de Zoología Aplicada (Madrid), Muséum National d'Histoire Naturelle (Paris), Natural History Museum (London), American Museum of Natural History (New York), and National Museum of Natural History (Washington). Data collected include label information, specimen identification, skull size and morphology, pattern of enamel in dentition, and pelage color and pattern.

As the scope of the taxonomic problem to be clarified here is restricted to hares previously identified as brown hares (*L. europaeus*) from Italy and Corsica, I excluded Italian *L. timidus* and the hares from Sardinia that belong to *L. mediterraneus*. I also excluded brown hare specimens collected after the end of the 19th century to avoid the influence of hare restocking. As far as I know, this has been a common practice in Italy for hunting purposes since the early 1900s, according to label data for specimens from the MF collection, with an increase in this activity after 1930 (Toschi 1965). Sample limits set in this paper are of interest both to define the natural distribution area of the brown hare in Italy and to characterize the indigenous population. Identification of brown hare specimens has been done using previous experience on Spanish hares (Palacios 1989).

As for the Corsican hare (*L. corsicanus*) all available specimens from the Italian Peninsula, Sicily, Corsica, and Elba Island were included in the sample. It contains specimens from the 19th century and a few from this century. The identification of the specimens was based on the characteristics of the holotype which was captured in Corsica and acquired in the market of Bastia. As regards the origin of this island population, there is evidence to support the view that hares were introduced. Vigne (1988) indicates that Corsican hares were probably released on the island no later than in the 16th century.

Only relative age class IV adult specimens (Caban-Raczynska 1964, Palacios 1989) were included in the comparison between samples. Some of the criteria used to identify the specimens with available skulls are: exoccipital-supraoccipital suture completely ossified and not detec-

table by color or thickness; mandibular capitulum well-ossified lacking porosity or fissures under the condyles; temporal tubercles and supraorbital processes well-developed; absence of porosity on the nasal lateral processes of the frontal bone and on the edges of the supraorbital processes. In specimens represented by skins only the relative age (adult, subadult, young) was estimated using other criteria based on the color and width of centrodorsal hair bands, body size (the dry measurements of hindfoot and ear were used when necessary), degree of ossification of long bones attached to skins, reproductive data, development of mammary nipples, etc.

As some of the old specimens in Italian collections are mounted with skull inside, not all the skulls of the specimens listed below were available for study. The Milan and Genova collections do not hold either specimens of *L. corsicanus* or old specimens of *L. europaeus*, but they have been examined to complete the information on contemporary specimens of *L. europaeus* and other hare species from neighboring areas. The Madrid collection was used as a reference for data on the Spanish species.

The *L. corsicanus* and *L. europaeus* specimens from Italy that were studied are listed in Appendix 1 and 2, respectively.

The available body measurements were taken from labels, and dry measurements were taken in some specimens on the stuffed skins with a digital calliper. Skull measurements were taken from all specimens using a standard digital calliper connected to a printer. Measurement abbreviations are listed in Appendix 3. To take some of the skull measurements calliper points were modified by sharpening them on both sides, and the longest ones were fluted transversely on the internal side near the far end; cranial foramina were measured using a set of wires of known diameter with an accuracy of 0.1 mm; external radius of curvature of the first upper incisor (I1/) measurements were taken using a circle template with accuracy of 0.1 mm; alveolar position of the I1/ end was determined by transparency using a lateral spotted light in a dark room; drawings of teeth in cross-section were made with camera lucida using refracted light, first upper incisor (I1/), second upper premolar (P2/), third upper premolar (P3/), and third lower premolar (P3) were drawn at the occlusal surface, and I1/ also in a cross-section, internal to the alveolus, located  $\frac{2}{3}$  of the total curvature posteriorly. Data on pelage color are limited to a comparison of centrodorsal hair bands in all the specimens with the underfur and the dominant hair considered separately, and observations of interspecies color variation in a number of body regions in some specimens of each species; pelage color was studied mainly from winter specimens by comparison with Ridgway's (1912) color table. Univariate statistics for the body and skull variables were computed with Statgraphics and BMDP software. The Levene test was used to determine if the variances were equal or unequal and, in the case of unequal variances, the Welch correction was used to calculate the test of hypotheses regarding the differences between means. The Chisquare analyses made to test differences in frequencies of skull and dental characters between species were performed using BMDP software. The correspondence factor analyses made to represent graphically the differences between species in frequency data of skull and dental characters were carried out using BIOMEKO software of the Centre Louis Emberger (CNRS, Montpellier). The stepwise discriminant analyses to calculate the taxonomic relationship among species using skull measurements were performed using BMDP software.

## Results

### External measurements

The body size of indigenous Italian hares is not well-documented because most of the old museum specimens lack external measurements. On the other hand, the few specimens of relative age IV that have external measurements, particularly in the sample of *L. corsicanus*, show a great disparity in the figures for each measurement (Table 1) that is hard to accept as intraspecies variation within *Lepus*. For instance, the tail length and hindfoot length have abnormally high variation coefficients, between 20 and 30 %. Figures for these coefficients in samples of other hare species



Table 1: External measurements of some adult *L. corsicanus* and *L. europaeus* specimens from Italy taken from skin labels. (1) indicates that the figures correspond to "lungheza mas.". In the other specimens they appear under the terms "testa et corpo" or "head and body length". Description of measurements is in Appendix 3.

Specimens	HB	T	HF	E
<i>L. corsicanus</i>				
BM 8.9.30.1	610	70	90	105
AMNH 160956	550	109	141	94.1
AMNH 160959	590	120	126	96
<i>L. europaeus</i>				
BM 98.10.2.18	550 (1)	90	130	107
BM 98.10.2.19	500 (1)	90	140	107
USNM 153400	558	92	138	112

from Spain of relative age IV have never been higher than 12 % for tail length and 4 % for hindfoot length (Palacios 1989).

The only explanation for this fact is that these measurements of Italian hares have been taken by each collector in a different way (tail length from base or from anus, with hair or without hair, or as the difference between total body length and head & body length; hindfoot with nail or without nail; ear from notch or from base).

As for hindfoot length, a control of the figure validity for *L. corsicanus* specimen BM 8.9.30.1 was done using the dry hindfoot length taken on the stuffed skin. As the figure for the dry measurement without nail is 123 mm and the foot is straight and seems intact, the available specimen label figure of 90 mm is not possible.

Other figures for dry hindfoot without nail in *L. corsicanus* are 118 and 120 mm in specimens BM 78.7.3.4 and BM 98.2.9.1, respectively. Considering that the hindfoot length without nail in hares undergoes an average decrease of 5.08 % from fresh to dry conditions ( $P < 0.001$ ,  $n = 33$ ,  $sd = 1.54$ ), it can be estimated that the fresh hindfoot length without nail of the three *L. corsicanus* specimens would range from 124 to 130 mm. On the basis of this estimate it is likely that the label figure of 141 mm available for the hindfoot length of specimen AMNH 160956 includes the nail.

De Winton's (1898) dry hindfoot measurement of the *L. corsicanus* holotype (BM 78.7.3.4) is 119 mm. This figure is similar to the dry measurement reported above, but the dry ear measurement (107 mm) was probably taken from the base as the dry figures from the notch that I took on the skin are 84 and 90.5 mm (right and left ear).

As regards *L. europaeus* from Italy, the size of the hindfoot seems somewhat larger than in *L. corsicanus*. The fresh hindfoot measurement of specimen USNM 153400 is 138 mm. This figure could be valid because the value for the dry measurement without nail is 134.8 mm. On the contrary, the figure of 130 mm corresponding to the specimen BM 98.10.2.18 seems somewhat low for relative age IV specimens of *L. europaeus* as we found equivalent figures in fresh specimens from Spain of relative age II (juveniles having the exoccipital-supraoccipital suture not yet ossified).

As for ear length, the available label figures for *L. corsicanus* 105, 94.1 and 96 mm, corresponding to specimens BM 8.9.30.1, AMNH 160956 and AMNH 160959, respectively, are smaller than those for *L. europaeus* with figures of 107, 107 and 112



mm corresponding to specimens BM 98.10.2.18, BM 98.10.2.19 and USNM 153400. This difference is also supported by the information derived from dry ear length figures taken from the notch in specimens of *L. corsicanus*. These measurements are 91, 84 and 90 mm in specimens BM 8.9.30.1, BM 78.7.3.4 and BM 98.2.9.1 and 84 mm in MNHN 1919-670. Considering that the ear length taken from the notch experiences a reduction of 10.2 % in hares from fresh to dry conditions ( $P < 0.001$ ,  $n = 59$ ,  $sd = 2.44$ ), the fresh measurement for those specimens can be estimated at between 92 and 100 mm, a range that is still less than that of *L. europaeus*.

The figures for head & body length of *L. corsicanus* (written on labels as “testa et corpo”) seem excessively large and it is likely that they, in fact, correspond to the total length measured from the front of the snout to the end of the tail. This assumption is supported by comparison with *L. europaeus*, a larger species in which, according to my data on other European populations, the head & body length of fresh adult specimens rarely attains figures over 550 mm, with figures between 530 and 550 mm being the norm.

The head and body length figures for the Italian sample of *L. europaeus* are still difficult to interpret. It depends on the exact meaning of the term “lungheza mas”, which is written on the labels of specimens BM 98.10.2.18 and BM 98.10.2.19 near the figures 550 and 500 mm. This term is probably the equivalent here to head & body length as the fresh measurements of total length in adult *L. europaeus* are rarely below 600 mm. However, a priori the meaning of “lungheza mas” seems to be different from the meaning of “testa et corpo” which appears on the labels of the other specimen, USNM 153400, before the figure of 558 mm.

In short, body size in *L. corsicanus* appears to be smaller than in *L. europaeus*, but interpretation of the scarce external measurements of the collection specimens entails some confusion, precluding their utilization for precise comparison between the two species. Body measurements of new *L. corsicanus* specimens would be of interest in the future for a full comparison with *L. europaeus*.

### Skull measurements

Skull size has been well-characterized on the basis of 29 measurements from two samples of ten specimens each of every species corresponding to relative age IV. These samples may be considered as few in number but are close to the maximum that can be gathered for study considering the specimens of indigenous hares of relative age IV from Italy (and collected during the 19th century) available worldwide. Tables 2 and 3 represent the values corresponding to the measurements of *L. corsicanus* and *L. europaeus*, respectively, and Table 4 depicts the results regarding univariate statistics.

*L. corsicanus* has a smaller skull than *L. europaeus* as is shown by most of the 29 measurements analyzed. In 9 of these measurements there is no range overlap between species. On the other hand, these measurements are very uniform and the values of the coefficients of variation are, in general, very small. In the case of the total length (TL) these coefficients are 2.9 % in *L. corsicanus* and 2.3 % in *L. europaeus*. The other variables have similar figures. For instance, as regards the palatal length (PL), they are 1.9 % and 4.0 %, respectively. The only one of these 9 variables with a large coefficient of variation is the height of processus muscularis mandibulae

Table 2: Skull measurements of 10 adult specimens of *L. corsicanus*. 1 — MF 10870, 2 — MF 10871, 3 — MF 11526, 4 — MF 11588, 5 — BM 8.9.30.1, 6 — BM 78.7.3.4, 7 — BM 98.2.9.1, 8 — BM 19.7.7.2341, 9 — AMNH 160956, 10 — AMNH 160959. The complete data for these specimens is in Appendix 1 and the description of skull measurements is in Appendix 3. Negative values of DIRSIM when the incisor root does not reach the suture and the value 0 when the posterior end of the incisor root reaches the level of the suture.

Variables	Specimens									
	1	2	3	4	5	6	7	8	9	10
TL	90.45	89.99	-	84.25	92.9	89.0	89.5	-	92.0	92.01
PL	35.8	36.5	37.12	34.87	36.3	36.1	35.6	37.0	36.23	37.18
INL	31.23	29.01	33.01	30.71	31.0	31.3	31.5	32.8	29.11	31.52
ENL	40.31	38.47	40.22	39.51	40.2	39.6	40.6	39.1	38.01	40.86
UCTRL	17.06	16.73	17.4	17.12	17.1	17.0	18.0	17.0	16.87	17.48
FIL	22.36	23.15	23.67	22.68	23.0	23.0	22.75	24.0	22.61	23.09
SFW	13.24	13.87	13.91	15.35	13.2	14.6	12.5	14.4	15.16	12.67
WSP	-	-	-	29.93	30.8	31.8	31.0	30.8	-	-
ANW	13.75	12.58	12.74	12.66	14.05	13.1	14.7	12.0	13.39	14.3
PNW	21.62	20.86	20.9	20.76	21.1	20.9	21.8	20.5	20.56	21.04
WFT	40.29	40.12	40.53	39.58	42.9	41.3	42.3	41.2	42.73	41.6
PZW	43.29	42.96	-	41.67	43.9	43.7	-	-	43.59	43.51
RW	25.17	25.49	26.26	25.15	26.9	26.0	26.3	26.7	27.33	26.77
FIW	9.66	11.02	10.93	11.21	11.35	10.75	11.25	11.6	10.72	9.52
NFB	6.87	6.76	7.17	6.22	6.75	6.6	5.9	7.0	7.1	7.43
PPW	10.36	10.12	10.06	10.62	11.45	10.3	10.8	10.4	9.57	10.18
FUISW	2.94	3.11	3.0	2.86	2.9	2.9	2.95	2.95	3.12	2.91
FUISL	1.95	1.9	1.82	1.78	1.85	1.65	1.8	1.7	1.93	1.84
RIC	9.6	10.7	10.6	10.0	10.2	10.8	11.5	10.3	10.3	10.7
FTL	7.85	7.59	7.97	8.56	8.2	7.8	8.8	9.7	9.79	8.0
TBL	10.84	10.13	-	11.23	11.15	10.2	11.0	-	10.66	11.19
TBW	7.79	7.39	-	6.58	7.5	7.0	7.6	-	8.03	8.11
DFZ	-	0.0	0.8	0.4	1.0	1.2	1.3	0.5	1.2	1.0
DFFP	0.3	0.3	0.5	0.3	0.4	0.2	0.4	0.6	0.6	0.4
MLCP	68.83	68.48	-	64.39	69.5	66.0	69.7	67.5	67.57	-
MH	40.45	39.68	-	37.12	40.4	37.9	40.2	39.5	40.74	-
LCTRL	18.27	17.92	18.16	18.39	17.8	17.9	19.0	18.15	17.48	-
HPMM	0.48	0.69	-	0.88	1.15	0.7	1.5	0.9	0.84	0.95
DIRSIM	-2.62	-2.38	-1.43	0.0	-1.5	-0.9	-0.7	-1.0	-0.5	0.0

(HPMM) which is 32.5 % in *L. corsicanus* and 8.4 % in *L. europaeus*. This is because the figures for this variable have values which are of the same or less than the difference between min. and max. values, particularly in *L. corsicanus* (mean value 0.89; range 0.48–1.5). Fig. 2, g illustrates well the shape of processus muscularis mandibulae in the two species.

Fig. 1 illustrates fairly well the important distinction between the two taxa as regards skull measurements. It corresponds to a three-dimensional plot where variables without overlap (HPMM, MLCP and INL) have been represented.

The differences in skull size are also backed by other variables which, although presenting some overlap, still differ significantly. Among them two variables are

Table 3: Skull measurements of 10 adult *L. europaeus* specimens. 1 — MF 10871 (dupl), 2 — MF 10872, 3 — MF 10874, 4 — MF 11523, 5 — MF 11525, 6 — MF 11527, 7 — BM 98.10.2.18, 8 — BM 98.10.2.19, 9 — BM 19.7.7.2486, 10 — USNM 153400. The complete data for these specimens is in Appendix 2 and the description of skull measurements is in Appendix 3.

Variables	Specimens									
	1	2	3	4	5	6	7	8	9	10
TL	97.47	102.2	96.42	96.49	98.43	97.29	95.31	97.08	95.29	100.8
PL	40.94	41.45	39.86	39.68	40.65	40.38	38.4	38.53	37.8	43.3
INL	38.73	35.16	42.74	37.97	39.55	33.5	37.09	38.27	34.11	40.29
ENL	44.92	42.16	45.36	44.6	47.81	41.44	44.75	45.03	41.65	47.21
UCTRL	17.81	18.46	18.83	18.1	17.38	17.23	16.27	17.96	17.73	18.33
FIL	26.36	26.68	24.4	25.48	26.75	25.29	26.2	25.79	24.08	28.35
SFW	13.45	16.0	14.51	16.07	13.75	14.87	14.76	13.9	14.32	13.2
WSP	32.92	35.55	-	39.01	34.1	34.91	34.46	34.95	34.69	36.84
ANW	15.39	15.72	16.15	-	14.5	14.93	13.98	17.02	14.86	16.56
PNW	21.92	22.35	21.2	23.99	22.53	22.21	22.16	23.8	22.3	25.1
WFT	41.19	43.85	44.37	43.25	43.19	44.02	42.06	41.9	42.4	42.76
PZW	43.67	45.92	46.43	45.98	45.86	47.78	44.29	43.15	45.44	46.57
RW	27.39	28.43	29.36	26.13	27.38	26.82	26.67	27.66	27.88	28.34
FTW	11.46	11.37	11.91	12.14	11.97	11.14	11.98	12.33	11.58	13.29
NPB	6.61	7.0	6.63	6.14	6.26	7.21	5.82	5.01	5.8	6.85
PPW	12.06	10.78	12.01	11.62	11.32	11.24	11.57	11.52	12.03	13.09
FUISW	3.04	-	3.2	2.93	2.99	3.01	2.85	3.23	2.94	3.2
FUISL	2.16	-	2.21	2.1	1.91	1.98	1.91	2.13	2.06	2.22
RIC	9.4	-	10.9	11.0	10.1	9.8	9.7	9.8	10.7	9.8
FTL	8.24	7.94	8.59	7.92	9.2	7.65	7.67	8.76	8.05	8.17
TBL	12.26	12.31	11.17	11.24	11.67	11.84	12.16	12.03	10.92	11.06
TBW	8.85	8.86	8.57	8.09	8.37	8.75	8.45	8.98	8.92	8.41
DFZ	0.3	0.2	0.7	0.3	0.2	0.3	0.9	0.6	0.0	0.0
DPPFP	0.8	0.8	0.9	0.9	0.8	0.8	0.6	0.8	0.7	0.8
MLCP	-	77.07	71.92	74.58	73.82	73.62	70.75	73.47	72.76	77.81
NH	-	43.33	41.16	41.64	41.02	41.34	42.63	44.17	43.05	45.11
LCTRL	-	18.7	19.28	19.48	19.17	18.79	17.5	18.56	17.65	18.99
HPMM	-	3.06	2.82	2.66	-	2.48	2.56	3.04	3.17	2.85
DIRSIM	-4.83	-3.53	-2.32	-4.31	-4.22	-3.76	-2.5	-4.21	-2.49	-5.74

noticeable: the distance between the end of the root of the first upper incisor and sutura incisivomaxillaris (DIRSIM) (Fig. 2, d) and the diameter of the posterior foramen palatinum (DPPFP). In both cases the overlap is very small, particularly in the second case which is reduced to the minimum, the highest value of *L. corsicanus* being the same as the smallest of *L. europaeus*.

In spite of the larger overall skull size for *L. europaeus*, there are a few variables which are larger in *L. corsicanus* than in *L. europaeus*. Among them, the narrowing of the palatine bridge (NPB), radius of the first upper incisor curvature (RIC), facial tubercle length (FTL), and diameter of foramen zygomaticus (DFZ) are worthy of note. These are the variables showing negative percentages of difference between spe-



Table 4: Univariate results corresponding to skull measurements of adult *L. corsicanus* and *L. europaeus*. Values of mean, range, coefficient of variation within each species, and statistical t, significance level, and % of difference between species are given. Variables marked with (1) have unequal variances; ns = difference between means is not significant ( $P > 0.05$ ); \* = somewhat significant ( $P < 0.05$ ); \*\* = significant ( $P < 0.01$ ); \*\*\* = very significant ( $P < 0.001$ ); (2) =  $P < 0.0001$ .

Variable	<i>L. corsicanus</i> (n=10)			t	sign. level	% d	<i>L. europaeus</i> (n=10)		
	mean	min-max	cv				mean	min-max	cv
TL	90.01	(84.25-92.9)	2.9	-6.57	*** (2)	8.5	97.67	(95.29-102.2)	2.3
PL (1)	36.27	(34.87-37.18)	1.9	-6.76	*** (2)	10.5	40.09	(37.8-43.3)	4.0
INL (1)	31.11	(29.01-33.01)	4.1	-6.63	*** (2)	21.3	37.74	(33.5-42.74)	7.6
ENL	39.68	(38.01-40.86)	2.3	-6.42	*** (2)	12.1	44.49	(41.44-47.81)	4.8
LCTRL	17.17	(16.73-18.0)	2.0	-2.46	*	3.7	17.81	(16.27-18.83)	4.0
FIL (1)	23.03	(22.36-24.0)	2.1	-6.90	*** (2)	12.5	25.93	(24.08-28.35)	7.4
SFW	13.89	(12.5-15.35)	6.4	-1.34	ns	4.2	14.48	(13.2-16.07)	6.7
WSP (1)	30.86	(29.93-31.8)	2.1	-5.32	***	14.2	35.27	(32.92-39.01)	4.9
ANW	13.32	(12.0-14.7)	6.4	-4.99	***	15.9	15.45	(13.98-17.02)	6.4
PNW (1)	21.00	(20.5-21.8)	1.9	-4.46	***	8.3	22.75	(21.2-25.1)	5.0
WFT	41.25	(39.58-42.9)	2.7	-3.39	**	3.9	42.89	(41.19-44.37)	2.3
PZW (1)	43.23	(41.67-43.9)	1.7	-3.86	***	5.2	45.50	(43.15-47.78)	3.0
RW	26.20	(25.15-27.33)	2.8	-3.65	**	5.3	27.60	(26.13-29.36)	3.4
FIW	10.80	(9.52-11.6)	6.3	-3.82	***	10.2	11.91	(11.14-13.29)	5.0
NPB	6.78	(5.9-7.43)	6.6	1.77	ns	-6.7	6.32	(5.01-7.21)	10.4
PPW	10.38	(9.57-11.45)	4.8	-5.28	*** (2)	12.9	11.72	(10.78-13.09)	5.2
FUISW (1)	2.96	(2.86-3.12)	2.7	-1.52	ns	2.7	3.04	(2.85-3.23)	4.2
FUISL	1.82	(1.65-1.95)	4.9	-5.14	*** (2)	13.7	2.07	(1.91-2.22)	5.3
RIC	10.47	(9.6-11.5)	4.8	1.33	ns	-3.2	10.13	(9.4-11.0)	5.7
FTL	8.42	(7.59-9.79)	9.2	0.71	ns	-2.4	8.21	(7.63-9.2)	5.9
TBL	10.80	(10.13-11.23)	3.9	-3.71	***	7.9	11.66	(10.92-12.31)	4.4
TBW	7.50	(6.58-8.11)	6.8	-5.85	*** (2)	14.9	8.62	(8.09-8.98)	3.3
DFZ	0.82	(0.0-1.3)	52.4	2.78	*	-57.3	0.35	(0.0-0.9)	82.8
DPFP	0.40	(0.2-0.6)	32.5	-7.73	*** (2)	97.5	0.79	(0.6-0.9)	10.1
MLCP	67.74	(64.39-69.7)	2.6	-6.20	*** (2)	9.1	73.97	(70.75-77.81)	3.0
MH	39.49	(37.12-40.74)	3.2	-4.63	***	7.8	42.60	(41.02-45.11)	3.3
LCTRL	18.11	(17.48-19.0)	2.3	-2.07	ns	3.1	18.68	(17.5-19.48)	3.6
HPMM	0.89	(0.48-1.5)	32.5	-14.49	*** (2)	217.9	2.83	(2.48-3.17)	8.4
DIRSIM	-1.10	(-2.62/0.0)	80.9	5.95	*** (2)	244.5	-3.79	(-5.74/-2.32)	29.2

cies in Table 4. Other variables showing the same tendency in relative terms as the above ones, but with absolute figures slightly smaller in *L. corsicanus* than in *L. europaeus*, are the smallest frontal width (SFW), the first upper incisor section width (FUISW), and the lower cheek tooth row length (LCTRL).

The variables showing the greatest percentage of difference between species are the DPFP, HPMM and DIRSIM.

### Skull characters

The skulls of *L. europaeus* and *L. corsicanus* are rather different in shape. *L. europaeus* generally has a massive skull with heavy structures while *L. corsicanus* has a light skull and the structures are more delicate than in the brown hare. The upper

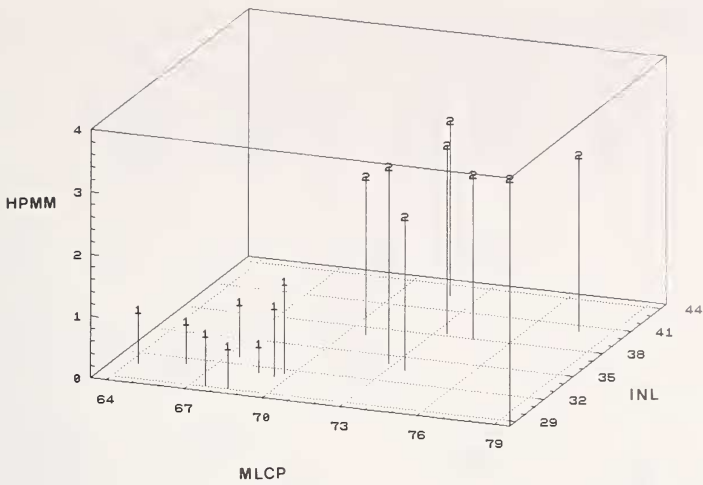


Fig. 1: Three-dimensional plot of variables without range overlap in adult *L. corsicanus* (1) and *L. europaeus* (2) showing the difference in size between these species.

contour of the skull from an lateral view in *L. europaeus* is straighter than in *L. corsicanus* which has a more rounded shape. This is mainly the effect of the nasals that are generally flat and long in *L. europaeus* and somewhat curved and shorter in *L. corsicanus*, as well as the brain case which in *L. corsicanus* is more rounded than in *L. europaeus*. However, most of the morphological difference between *L. corsicanus* and *L. europaeus* is the result of the influence of a number of skull structures related to 15 different characters, which are compared in the two species below. The character states presented by each specimen are shown in Tab. 5.

**A) Position of the lateral foramen palatinum** (Fig. 2, a, 1). — In *L. corsicanus* specimens these foramina are normally visible on the ventral plate of the palatine process of the maxilla, near the P2/ (state 1). Some specimens of *L. corsicanus* have a second pair of foramina occupying the position defined below as typical for *L. europaeus*, or in an intermediate site (state 2) between the position typical for *L. europaeus* and the position defined as state 1. Most of the specimens of *L. europaeus* have these small foramina on the anterior edge of the palatine process of the maxilla, positioned laterally (state 3). This site is internal to the incisive foramina and is not visible from the perpendicular to the skull in ventral position. *L. europaeus* specimens with a second pair of foramina near P2/ or in an intermediate position are not common.

**B) Position of the posterior foramen palatinum** (Fig. 2, a, 2). — Most *L. corsicanus* specimens have these foramina totally enclosed in the lamina horizontalis of the palatine bone (state 1) while in *L. europaeus* these foramina are positioned exactly on the suture separating the lamina horizontalis from the palatine process of the maxilla (state 3). A few specimens of *L. corsicanus* have these foramina in an intermediate position that is close to state 1, but with the lamina horizontalis opened in front to the suture (state 2). The lamina horizontalis is more extensive in *L. corsicanus* than in *L. europaeus* and in many specimens of *L. corsicanus* it is slightly pitted, this being another distinction from *L. europaeus* which never has a pitted lamina horizontalis.

**C) Symphysis of the incisive bone** (Fig. 2, h). — *L. corsicanus* specimens normally have a small but well-developed crest on the top of the anterior part of this symphysis (state 1), while

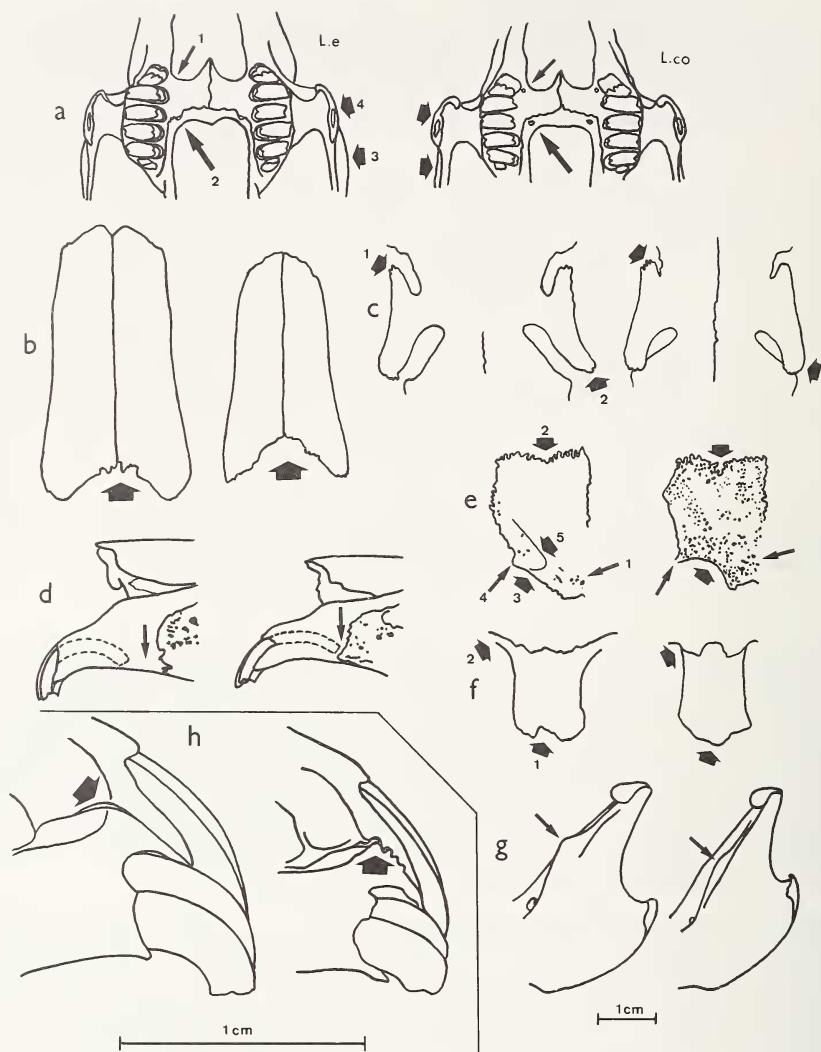


Fig. 2: Detail of several skull characters with different shapes in adult *L. europaeus* (left) and *L. corsicanus* (right). a: 1 — position of the lateral palatal foramina, 2 — position of the posterior palatal foramina, 3 — upper edge of canalis zygomaticus, 4 — shape of the facial tubercle; b: shape of the fronto-nasal suture; c: 1 and 2 — shape of the oral and aboral part of the supraorbital process; d: position of the end of the first upper incisor root with respect to the incisivo-maxillaris suture; e: 1 — pitted degree in parietal surface, 2 — shape of the coronary suture, 3 — posterior contour of the parietal, 4 — parietal projection between temporal and occipital bones, 5 — parietal trench; f: 1 and 2 — posterior contour and lateral margins of the medial parietal part of squama ossis occipitalis; g: shape of processus muscularis mandibulae; h: symphysis of the incisive bone. Drawings of *L. europaeus* correspond to specimen USNM 153400 and drawings of *L. corsicanus* correspond to specimens BM 98.2.9.1 (a, d), BM 78.7.3.4 (b, e), BM 8.9.30.1 (c, f, g), and MNHN 1962-2546 (h).



Table 5: Skull character states of adult *L. corsicanus* and *L. europaeus* specimens. Characters represented by uppercase letters and states (1, 2, 3) are described in the text.

<i>L. corsicanus</i>		Characters													
Specimens	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
MF 10870	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2
MF 10871	1	3	1	1	1	1	1	1	2	3	1	1	1	2	1
MF 11526	1	1	1	1	2	-	-	-	2	-	-	1	3	-	1
MF 11588	1	1	1	1	1	2	1	3	2	1	3	1	2	1	1
BM 8.9.30.1	1	2	1	1	1	1	1	1	1	1	2	2	1	1	2
BM 78.7.3.4	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1
BM 98.2.9.1	1	1	1	1	2	2	1	1	1	2	1	1	1	2	2
BM 19.7.7.2341	2	1	1	1	2	1	-	-	1	-	1	1	1	-	1
AMNH 160956	3	1	1	1	2	1	-	1	2	1	2	1	1	2	1
AMNH 160959	1	1	1	-	1	1	1	1	1	1	2	1	1	1	1
<i>L. europaeus</i>		Characters													
Specimens	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
MF 10871 dupl	3	3	3	3	3	2	3	2	2	3	3	1	1	2	1
MF 10872	3	3	2	3	3	3	3	2	3	3	3	1	3	3	3
MF 10874	1	3	3	3	3	2	3	3	2	3	3	3	1	3	3
MF 11523	3	3	3	3	3	3	3	3	3	3	2	3	3	3	2
MF 11525	3	3	1	3	2	3	3	2	2	2	2	3	3	3	3
MF 11527	3	3	1	3	3	2	2	2	3	3	3	3	3	3	3
BM 98.10.2.18	3	3	3	3	3	2	3	2	2	3	3	3	2	3	1
BM 98.10.2.19	3	3	3	3	3	3	3	3	2	3	3	1	3	2	2
BM 19.7.7.2486	3	3	3	3	2	3	3	2	3	3	2	1	3	2	1
USNM 153400	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2

in *L. europaeus* this symphysis is normally smooth without a crest (state 3). The specimens having a slightly developed crest have been defined as state 2.

**D) Shape of the supraorbital processes.** — In *L. corsicanus* the oral parts of these processes (Fig. 2, c, 1) are generally short and parallel, being frequently fused with the frontal bone, and the aboral parts (Fig. 2, c, 2) are only somewhat divergent backwards (state 1); in *L. europaeus* the oral parts are larger than in *L. corsicanus* and are rarely fused with the frontal bone being frequently divergent forwards, and the aboral parts are greatly divergent backwards (state 2).

**E) Fronto-nasal suture** (Fig. 2, b). — The shape of this suture in *L. corsicanus* is generally like a deep inverted open V with straight or slightly concave sides due to the fact that the lateral posterior ends of the nasals are usually sharp and because the frontal bone protrudes noticeably between the nasals (state 1); in *L. europaeus* the fronto-nasal suture has the shape of an open W in right position with more rounded posterior nasal ends and small frontal bone projection (state 3). The intermediate specimens have been characterized as state 2.

**F) Parietal surface** (Fig. 2, e, 1). — In *L. corsicanus* the parietal surface is normally very pitted (state 1), while in *L. europaeus* it is smooth or slightly pitted (state 3). The intermediate specimens have been characterized as state 2.

**G) Posterior contour of the medial parietal part of the squama ossis occipitalis** (Fig. 2, f, 1). — In *L. corsicanus* there usually is a medial projection backwards (state 1) while in *L. europaeus* there is a medial notch, often with a slight pointed projection inside (state 3). The specimens with a straight contour have been typified as state 2.

H) **Lateral margins of the medial parietal part of the squama ossis occipitalis** (Fig. 2, f, 2). — In *L. corsicanus* the lateral margins are rather parallel and anteriorly reach the parietals at the same level (state 1), while in *L. europaeus* the lateral margins diverge markedly forwards and in most cases the anterior ends remain at a lower level than the parietals (state 3). Specimens having parallel margins with anterior ends not reaching the parietals and terminating at a lower level, or having very divergent margins reaching the parietals anteriorly at the same level have been typified as state 2.

I) **Caudal groove of the coronary suture** (Fig. 2, e, 2). — The groove that each parietal has anteriorly is generally very marked in *L. corsicanus* (state 1) and slight in *L. europaeus* (state 3). The intermediate cases have been typified as state 2. It is also noteworthy that in *L. europaeus* the anterior-internal part of the parietals protrudes more forwards into the frontal bone than in *L. corsicanus*.

J) **Posterior contour of the parietal** (Fig. 2, e, 3). — In *L. corsicanus* the portion of the parietal contour that is in contact with the occipital is generally concave (state 1), while in *L. europaeus* this portion is usually straight (state 3). The intermediate cases have been typified as state 2.

K) **Parietal projection between temporal and occipital bones** (Fig. 2, e, 4). — *L. corsicanus* usually has a narrow parietal projection separating the temporal and occipital bones (state 1) or a parietal entrant only (state 2); as regards *L. europaeus* only a few specimens display state 2, and the most common case is the occipital and the temporal bones in close connection without a projection or entrant between (state 3).

L) **Upper edge of canalis zygomaticus** (Fig. 2, a, 3). — In *L. corsicanus* the upper edge of canalis zygomaticus is usually not prominent (state 1) or there is a slightly developed crest (state 2), while in *L. europaeus* generally there is a markedly developed crest (state 3).

M) **Presence/absence of lateral foramina on the zygomatic process of the maxilla.** — In *L. corsicanus* there usually is a small foramen above the crista facialis, anterior to the large zygomatic foramen (state 1), but in most specimens of *L. europaeus* there is no foramen (state 3); the specimens with diminutive cavities but no real foramen have been typified as state 2.

N) **Postero-external parietal furrow** (Fig. 2, e, 5). — In *L. europaeus* there usually is a well-marked lateral longitudinal furrow on the parietal surface close to the junction with the occipital and temporal bones (state 3). This furrow is usually absent (state 1) or slightly marked (state 2) in *L. corsicanus*.

O) **Shape of the incisive foramina.** — In *L. corsicanus* the incisive foramina usually have divergent margins along the first  $\frac{2}{3}$  of their length, and parallel lateral margins along the posterior  $\frac{1}{3}$  (state 1); this shape is basically similar in *L. europaeus* except that in this species there is usually a subterminal enlargement approximately  $\frac{2}{3}$  of the incisive foramina length posteriorly, the foramina being wider at this point than at the posterior end (state 3). Specimens with only a slight enlargement have been typified as state 2.

Among the other noticeable features distinguishing the two species, the shape of the facial tubercles (Fig. 2, a, 4) is worthy of note. They are more divergent posteriorly protruding more outwards in *L. corsicanus* than in *L. europaeus* in which they are fairly parallel. The fact that the facial tubercles are more external in *L. corsicanus* than in *L. europaeus* is supported by values of the TL/WFT index for which the means, 2.17 in *L. corsicanus* and 2.26 in *L. europaeus*, show a fairly significant difference ( $P < 0.01$ ). The length of the facial tubercle also presents values that are relatively larger in *L. corsicanus* than in *L. europaeus* (means of TL/FTL index 10.87 and 11.91, respectively,  $P < 0.05$ ).

The statistical comparison of the frequencies of the character states in the two species is presented in Table 6. Figures of  $X^2$  (Chisquare) and the significance level are given. High values of  $X^2$  and small probabilities in 8 characters suggest that the frequencies corresponding to the two species make a significant difference between

Table 6: Statistical comparison of frequencies corresponding to the skull character states of *L. corsicanus* and *L. europaeus*. Frequencies for each character can be easily obtained in Table 5.

Character	X <sup>2</sup>	Significance level
A	12.844	**
B	16.364	***
C	13.333	***
D	19.000	*** (2)
E	15.200	***
F	13.652	***
G	14.936	***
H	14.760	***
I	11.111	**
J	14.355	***
K	7.969	*
L	8.923	*
M	8.100	*
N	11.925	**
O	5.600	ns

them. The most remarkable differences lie in the position of the posterior foramen palatinum and the shape of the supraorbital processes.

The results of a factor correspondence analysis based on the frequencies corresponding to the 15 skull characters in each species are plotted in Fig. 3. This plot corresponds to the projection on axes 1 and 2 that displays the maximum difference between species. The projections belonging to the specimens are enclosed in the contour line and indicate that the two taxa are separated without overlap. Axis 1 explains 36.08 % of the variance and contributes most to species differentiation, character states D1, D3, H1, J1, F1, G1, and G3 being, in that order, the most important. Axis 2 only explains 9.64 % of the variance, E2, O2, B2, L2, J2, O1, and H3 being the most important character states. States 1 are typical of *L. corsicanus*, states 3 are typical of *L. europaeus*, and states 2 have small frequencies shared by the two species or appearing exclusively in only one species. According to Fig. 3 the most typical specimens in the case of *L. corsicanus* are ch, ce, ca, cj, and cf, and eb, ej, ee, ef, and ed in the case of *L. europaeus*. All these specimens are the most distant on the plot and are projected near the states that are more important in the separation, particularly those related to axis 1.

### Dental characters

The morphological pattern of enamel in the dentition of *L. europaeus* and *L. corsicanus* was studied on the basis of the characters of I1/, P2/, P3/ and P/3 cross-sections. The general characteristics of these teeth are rather similar in the two species as is the rule among species of the genus. I1/ is rectangular with a shallow anterior sub-central simple groove separating two lobes which have a circular contour, the lingual one being only somewhat narrower than the labial one. P2/ has a triangular-like shape with three main anterior grooves, being from right to left in a right tooth mesoflexus, paraflexus (the deepest one), and hypoflexus. These main entrants are, respec-



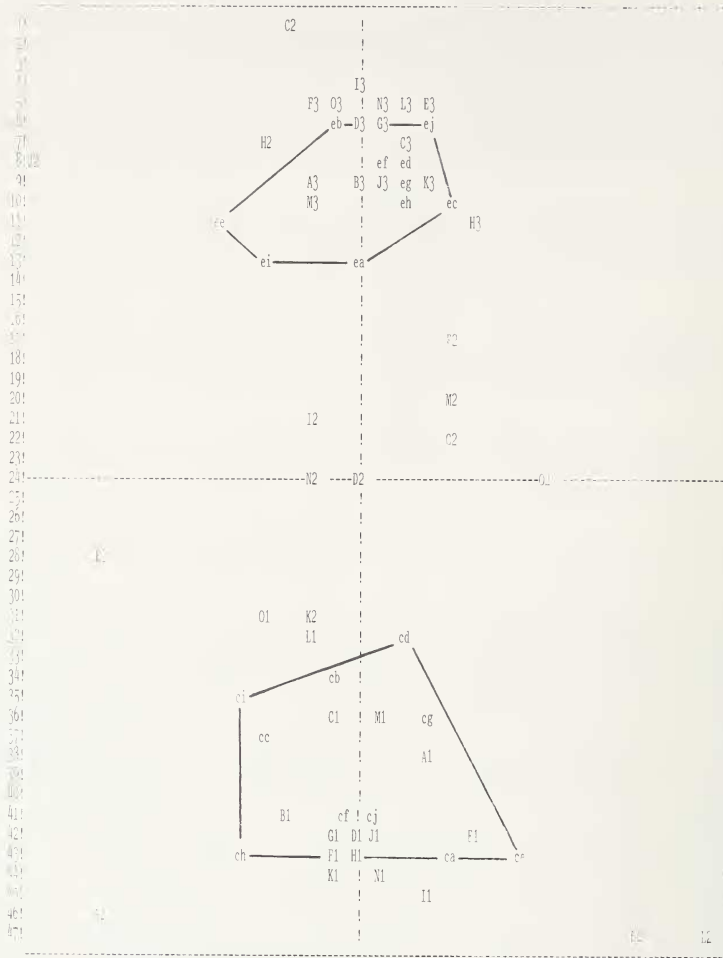


Fig. 3: Projection of the frequencies corresponding to the skull character states of *L. corsicanus* and *L. europaeus* specimens in relation to axes 1 (vertical) and 2 (horizontal) of the correspondence factor analysis. Couples of lower case letters represent the specimens of each species (e = *L. europaeus*; c = *L. corsicanus*; a, b, c . . . = same specimens and order as in Table 5) and upper case letters followed by numbers 1, 2, 3 represent the skull character states.

tively, between postcone and lagicone, lagicone and mesial hypercone, and mesial hypercone and distal hypercone. P3/ is also rectangular with a noteworthy transversal groove, the hypoflexus, that is open on the lingual side and crosses the tooth from one side to the other nearly reaching the labial wall. The hypoflexus has a fluted enamel structure especially on the anterior edge. Finally, P3/ has a subcircular shape with a deep anteroflexid separating anteriorly the two anteroconids, a slight but wide protoflexid on the labial side separating the labial anteroconid of the protoconid, and a long transversal hypoflexid open to the labial side that nearly reaches the lingual

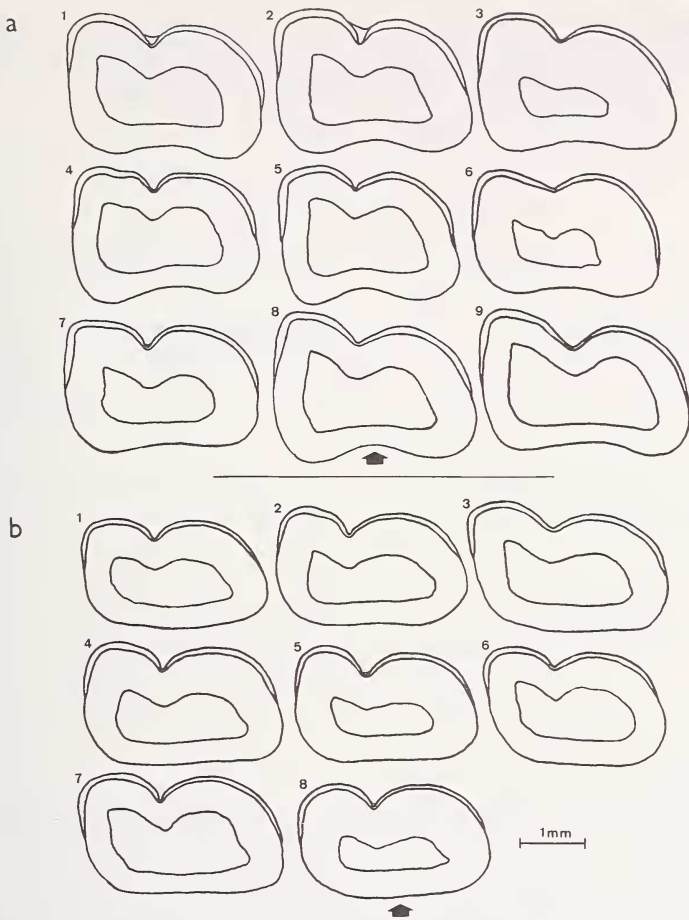


Fig. 4: Posterior cross section of several first upper incisors of adult *L. europaeus* (a) and *L. corsicanus* (b). a: 1 — MZ 10871 (dupl), 2 — MZ 10873; 3 — MZ 10874, 4 — MZ 11523, 5 — MZ 11524, 6 — MZ 11525, 7 — MZ 11527, 8 — MZ 11597, 9 — MZ 11598; b: 1 — BM 78.7.3.4, 2 — MZ 10870, 3 — MZ 10871, 4 — MZ 11526, 5 — MZ 11588, 6 — INBS 3830, 7 — AMNH 160956, 8 — AMNH 160959. The arrow points to the posterior contour of the section which has a different shape in each species.

wall and separates the protoconid from the hypoconid. The lingual and posterior margins of this tooth are normally rounded, lacking any entrant except for the small paraflexid that is located in antero-lingual position.

Despite the general resemblance of *L. europaeus* to *L. corsicanus*, there are some dental characters that allow a distinction to be made. Below I describe seven characters. Specimen data are summarized in Table 7.

**A) Posterior contour of the I1/ cross-section (Fig. 4).** — The shape of this tooth determines one of the biggest morphological differences between *L. europaeus* and *L. corsicanus* and also enables us to distinguish between *L. corsicanus* and many other hare species. In *L. corsicanus*

Table 7: Dental character states of adult *L. corsicanus* and *L. europaeus* specimens. Characters represented by uppercase letters and states 1, 2, 3 are described in the text; columns r and l correspond to the right and left teeth. Asterisks indicate specimens belonging to relative age class III which have been added to increase the samples in both species.

<i>L. corsicanus</i>														
Specimens	Characters													
	A		B		C		D		E		F		G	
	r	l	r	l	r	l	r	l	r	l	r	l	r	l
MF 10870	2	2	1	1	1	-	1	1	1	1	1	1	1	1
MF 10871	1	1	1	1	-	1	1	1	1	1	1	1	1	1
MF 11526	1	1	1	1	1	-	1	1	1	1	1	1	1	2
MF 11588	1	1	1	1	1	-	1	1	1	2	1	1	1	1
BM 8.9.30.1	-	-	3	2	1	-	1	-	1	-	1	-	3	-
BM 78.7.3.4	1	1	1	1	1	-	1	1	2	1	1	1	1	1
BM 98.2.9.1	-	-	1	1	-	1	1	1	1	1	1	1	1	1
BM 19.7.7.2341	-	-	1	1	1	-	1	1	1	1	1	1	3	3
AMNH 160956	1	1	2	1	1	-	2	2	1	2	1	1	1	1
AMNH 160959	1	1	1	1	1	-	1	1	2	2	2	2	1	1
INBS 3830 *	1	1	1	1	1	-	1	1	1	1	1	1	1	1

<i>L. europaeus</i>														
Specimens	Characters													
	A		B		C		D		E		F		G	
	r	l	r	l	r	l	r	l	r	l	r	l	r	l
MF 10871 dupl	3	3	3	2	1	-	-	-	-	-	-	-	-	-
MF 10872	-	-	1	3	3	-	3	3	1	1	2	2	1	1
MF 10874	3	3	3	3	3	-	3	3	3	3	1	1	1	1
MF 11523	3	3	3	3	1	-	1	2	2	2	2	1	3	1
MF 11525	3	3	3	3	1	-	3	3	3	3	3	3	3	3
MF 11527	3	3	3	3	-	3	1	1	2	2	3	3	2	1
BM 98.10.2.18	-	-	3	3	3	-	3	3	2	3	1	2	3	3
BM 98.10.2.19	-	-	3	3	2	-	2	2	1	2	1	2	1	1
BM 19.7.7.2486	-	-	3	3	-	1	1	1	3	2	1	1	1	1
USNM 153400	-	-	3	3	3	-	1	1	3	3	1	2	3	3
MF 10873 *	3	3	-	-	2	-	3	2	1	2	3	2	3	3
MF 11524 *	3	3	3	3	1	-	3	-	2	-	1	-	3	-
MF 11597 *	3	3	2	2	1	-	3	3	1	3	3	3	3	3
MF 11598 *	3	3	3	3	3	-	3	3	1	1	3	2	2	2

the posterior contour of the cross-section of this tooth is generally flat or slightly convex (state 1) while in *L. europaeus* it is always concave (state 3). The slightly concave morphotype (state 2) is very rare in *L. corsicanus*.

B) **Size of postcone and lagicone of P2/** (Fig. 5, a). — This character represents another important difference between the two species. In most specimens of *L. corsicanus* the postcone protrudes farther than the lagicone (state 1) while in specimens of *L. europaeus* the postcone usually protrudes less than the lagicone (state 3). State 2 representing specimens of both species in which both lagicone and postcone protrude to the same degree is very rare.

C) **Crenulation on the posterior edge of the P3/ hypoflexus** (Fig. 5, b). — In *L. europaeus* there frequently is a deep and oblique entrant on the posterior edge of the P3/ hypoflexus,



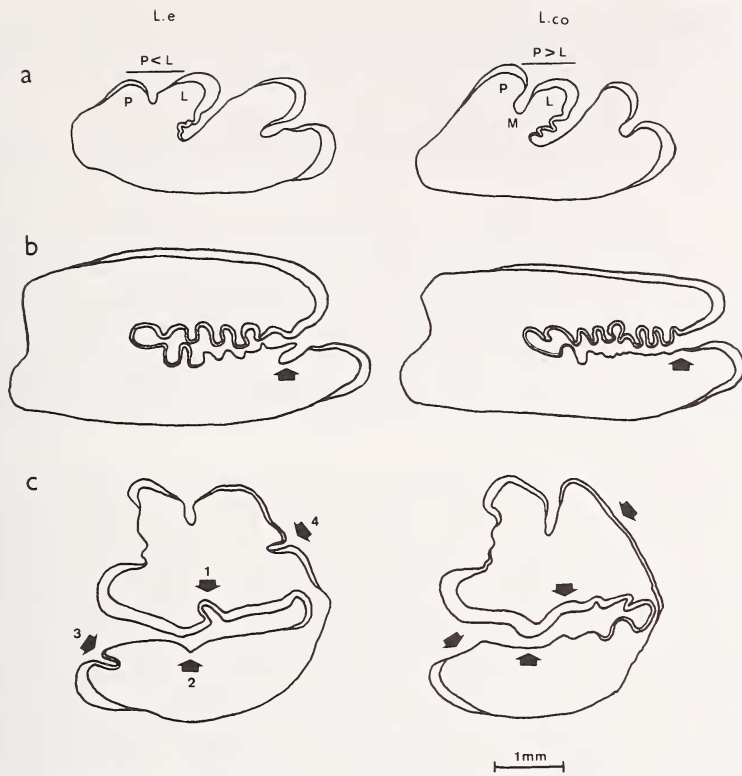


Fig. 5: Details of the occlusal surface of the second upper premolar (P2/), third upper premolar (P3/), and third lower premolar (P/3) of adult specimens of *L. europaeus* and *L. corsicanus* showing some dental characters of taxonomic relevance. a: P2/ (right side) P = postcone, L = lagicone, M = mexoflexus; b = P3/ (right side) the arrow shows the crenulation of the posterior edge of the P3/ hypoflexus; c: P/3 (left side) 1 = centroflexid on the anterior edge of the P/3 hypoflexid, 2 — slight crenulation on the posterior edge of the P/3 hypoflexid, 3 — crenulation on the internal side of the P/3 hypoconid, 4 — paraflexid on the antero-lingual border of P/3. Drawings of *L. europaeus* (left) correspond to specimens MZ 11525, USNM 153400, MZ 11525, and drawings of *L. corsicanus* (right) correspond to specimens MZ 11588, MZ 11526, and BM 78.7.3.4, from above to below, respectively.

oriented through the opening of the groove (state 3), while this deep crenulation was not found in *L. corsicanus* (state 1). Two specimens of *L. europaeus* show a slight crenulation (state 2).

D) **Centroflexid on the anterior edge of the P/3 hypoflexid** (Fig. 5, c, 1). — *L. europaeus* sometimes has a large centroflexid (state 3) and normally a smaller but differentiated centroflexid (state 2) occupying a medial position on the anterior edge of the P/3 hypoflexid. This groove appears to be a different structure from the typical inflexion shown by hares resulting from the primitive connection between trigonid and talonid. In most cases, *L. corsicanus* lacks the centroflexid (state 1), while state 3 was not found in this species.

E) **Slight crenulation on the posterior edge of the P/3 hypoflexid** (Fig. 5, c, 2). — In *L. europaeus* there frequently is a small but well-defined crenulation occupying a central position on the posterior edge of the P/3 hypoflexid (state 3) while in *L. corsicanus* this crenulation is normally absent (state 1), being slightly apparent (state 2) in very few cases.

F) **Crenulation on the internal side of the P/3 hypoconid** (Fig. 5, c, 3). — *L. europaeus* may exhibit a deep and oblique entrance on the internal side of the P/3 hypoconid (state 3), oriented to the hypoflexid opening. This entrance is normally absent in *L. corsicanus* (state 1) and, if present, is never deep (state 2).

G) **Paraflexid or parafoetid on the antero-lingual border of P/3** (Fig. 5, c, 4). — The frequency in *L. europaeus* of a deep paraflexid or parafoetid in P/3 (state 3) was double that in *L. corsicanus* which lacks the paraflexid in most cases (state 1). Cases of slight paraflexid (state 2) were rare in both species.

Another morphological difference found between the two species as regards dentition is also related to the shape of the I1/ cross section. In *L. europaeus* the shape is more square while in *L. corsicanus* it is more rectangular (Fig. 4). The difference is due to the fact that *L. corsicanus* has relatively larger measurements of first upper incisor section width (FUISW) than *L. europaeus*, while the figures for section length (FUISL) are correlated with skull size. This point is supported by the data in Table 4 showing that there is a strong overlap in FUISW values while the means for FUISL differ very significantly.

The statistical results of the comparison of the frequencies of dental characters for each species are presented in Table 8 where figures of  $X^2$  and significance level are given. Two of the seven characters studied have high  $X^2$  values and low probabilities suggesting that the frequencies corresponding to the two species make a significant difference between them. These characters are the posterior contour of the I1/ cross section and the size relationship between postcone and lagicone of P2/.

The results of a factor correspondence analysis based on the frequencies table corresponding to the 7 dental characters in each species are plotted in Fig. 6. This plot corresponds to the projections on axes 1 and 2 that display the maximum difference between species. The projections belonging to the specimens are enclosed in the contour line and it can be seen that the two taxa are separated without overlap. Axis 1 explains 30.78 % of the variance and contributes most to species differentiation, character states B1, A1, A3, D3, F1, and B3 being the most important in that order. Axis 2 explains 16.88 % of the variance, B2, C2, F3, F2, D2, E3, and E2 being the most important character states. States 1 are typical of *L. corsicanus*, states 3 are typical of *L. europaeus*, and states 2 are those with small frequencies shared by the two species or appearing exclusively in only one species. According to Fig. 6 the most typical specimens of each species are ci, ca, cb, and cg in the case of *L. corsicanus*

Table 8: Statistical comparison of frequencies corresponding to the dental character states of *L. corsicanus* and *L. europaeus*. Frequencies used for the analysis correspond to columns Ar, Bl, Cr+1, Dr, Er, Fr, and Gr, which have the minimum number of missing data.

Character	$X^2$	Significance level
A	17.000	***
B	21.315	*** (2)
C	9.244	**
D	10.478	**
E	5.682	ns
F	5.400	ns
G	4.308	ns

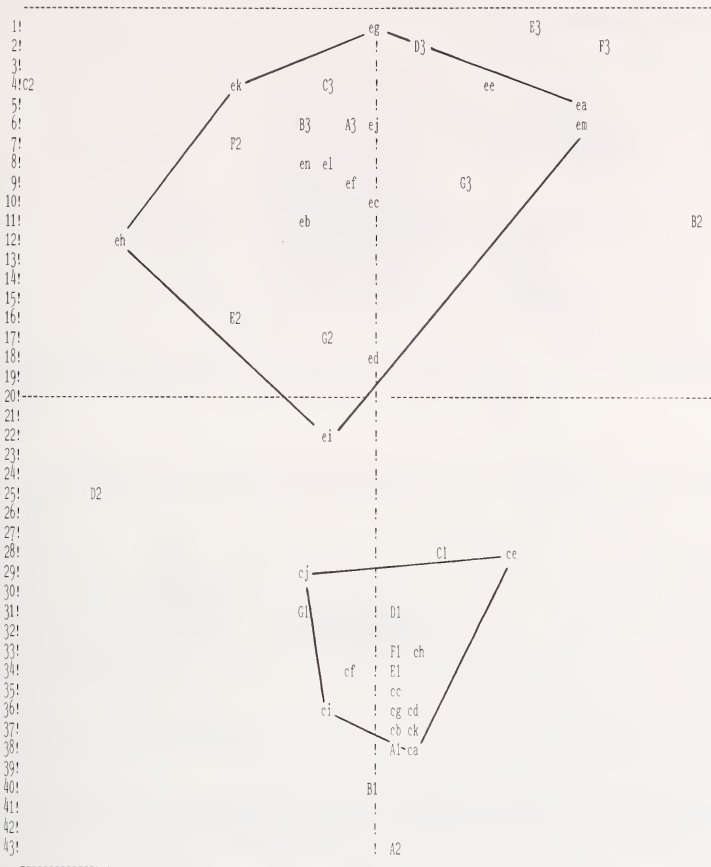


Fig. 6: Projection of the frequencies corresponding to the dental character states of *L. corsicanus* and *L. europaeus* specimens in relation to axes 1 (vertical) and 2 (horizontal) of the correspondence factor analysis. Couples of lower case letters represent the specimens of each species (e = *L. europaeus*; c = *L. corsicanus*; a, b, c . . . = same specimens and order as in Table 7) and upper case letters followed by numbers 1, 2, 3 represent the projections of the dental character states.

and ek, ea, em, ee, and eg in the case of *L. europaeus*. All these specimens are the most distant in the plot and are projected near the more important states in the separation, particularly those related to axis 1.

**Pelage characters**

*L. europaeus* and *L. corsicanus* differ in several pelage characters of taxonomic importance although the overall appearance of these two species seems fairly similar. Information regarding this chapter is complete only for the color of the centrodorsal hair for which the data were taken for the whole set of specimens of the two species. For the other characters the analysis is based on data of some specimens chosen as representative of those belonging to each species.

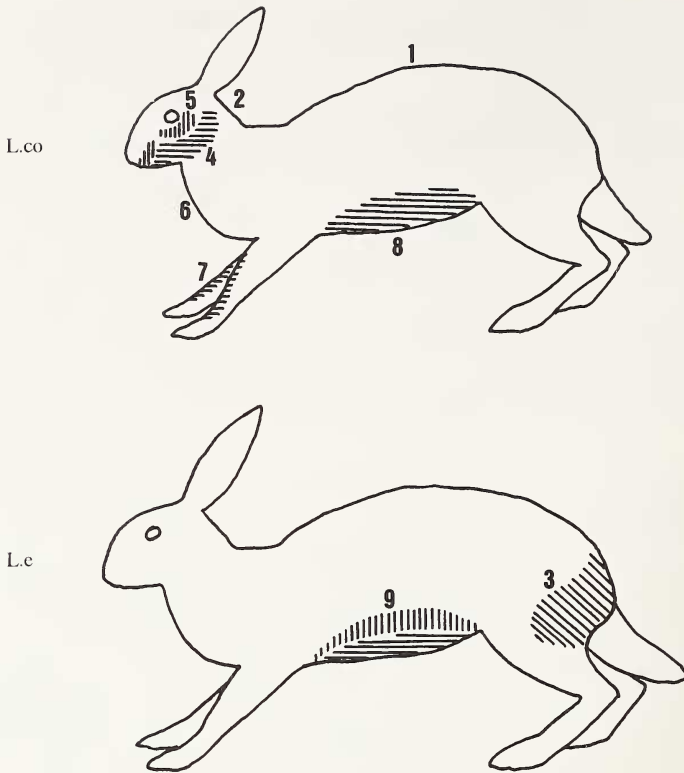


Fig. 7: Position of different winter pelage characters of taxonomic relevance to distinguish between adults of *L. corsicanus* and *L. europaeus*. 1 — centrodorsal hair, 2 — nape, 3 — rump, 4 — facial band, 5 — subocular patch + whiskers patch, 6 — collar, 7 — inner surface of forelimbs, 8 — ventral white, 9 — transitional fringe between back and belly. See comments in text.

A) **Centrodorsal hair** (Fig. 7, 1). — As regards the color of the centrodorsal hair, there are differences in the dominant hair bands as well as in the underfur bands, but the dominant hair has some variation in *L. corsicanus* and only the underfur color provided definitive conclusions on the species distinctiveness.

1) **Dominant hair.** — As indicated above, analysis of dominant hair needs further study but there are some differences which deserve to be typified now. The adults of the two species are very similar with respect to the length and the color of the bands, except at the base of the hair. In the upper part of the hair there is a black tip which is common to the two species; below there is a subterminal ring that is pinkish buff in *L. corsicanus* and cream buff in *L. europaeus*, and then there is a wide fringe of black color occupying the middle part of the hair, which is also present in the two species. Under this black central zone, in *L. corsicanus* there is a narrow pinkish buff band and below is the base of the hair which is white, sometimes with a slight brown tone. The last two bands are present on *L. corsicanus* specimens MF 11526, MF 11590, BM 78.7.3.4, BM 98.2.9.1, AMNH 160959, MNHN 1919-670. The specimens belonging to *L. europaeus* always have a long grey base under the central black band. However, the dominant hair has some variability in *L. corsicanus*, and some specimens have a pale grey base (MF 10870, MF 11588, MF 10871, MF 11592 and AMNH 160956). It is likely



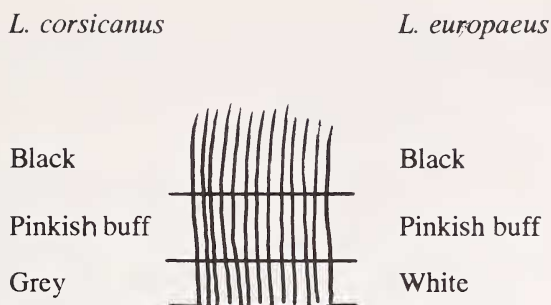


Fig. 8: Drawing that illustrates the color characteristics of the underfur of *L. corsicanus* and *L. europaeus* adults in winter pelage. The color of the base is a discriminant character between the two species.

that there is a moulting, seasonal or age influence on this character. It may also be a polymorphic character. Thus, the current state of knowledge does not allow species separation in all specimens.

2) Underfur (Fig. 8). — The adult specimens of *L. corsicanus* have three well-differentiated bands, the grey basal one, the intermediate pinkish buff band with some cinnamon-buff effect, and the black upper band. All *L. corsicanus* specimens conform to this description which can be checked in specimens MZ 10870, MF 10871, MF 11526, MF 11588, MF 11590, MF 11592, BM 78.7.3.4, BM 98.2.9.1, MNHN 1919-670, AMNH 160956, and AMNH 160959.

As regards the underfur color of *L. europaeus*, most of the adult specimens have two well-defined bands, the white basal one and the upper band which is black. In a few specimens there is a third band positioned between the other two but hardly detectable. It is of the same color as the medial band of *L. corsicanus* but is less marked than in the latter species. The underfur color description of *L. europaeus* can be checked in specimens MZ 10872, MF 10874, MF 11585, MF 11586, MF 11591, MF 11594, MF 11595, BM 98.10.2.18, BM 98.10.2.19, and USNM 153400. The *L. europaeus* specimens with a somewhat perceptible medial pinkish buff band are MF 11585, MF 11586.

It is likely that the old skins of *L. europaeus* may have partially or totally lost the color of the intermediate band of the underfur which is normally rich in color in fresh specimens. However, there could be a big difference between *L. corsicanus* and *L. europaeus* as regards this intermediate band. Comparing old skins of the two species in the MZ collection stored under the same conditions for over one hundred years, all the specimens belonging to *L. corsicanus* still display a wide and richly colored band while in *L. europaeus* this band is scarcely perceptible or absent.

Looking at the base of the centrodorsal hair of adult specimens, in *L. europaeus* the contrast between the white base of the underfur and the grey base of the dominant hair is noteworthy, and in *L. corsicanus* the contrast between the grey base of the underfur and the white base of the dominant hair, except in specimens of *L. corsicanus* with a grey base in the dominant hair.

However, the color of the base of the underfur is a stable and discriminant character and, consequently, very useful for differentiating between adult specimens of *L. europaeus* and *L. corsicanus*. Juvenile *L. europaeus* also have a grey base in the underfur, as is the case, for instance, in specimens MF 11584, MF 11587. The grey color must turn to white at an early stage in *L. europaeus*. The specimen USNM 153399, belonging to relative age III, already has a white base.

B) Nape (Fig. 7, 2). — There is a very noticeable difference between the two species as regards nape color bands. In *L. corsicanus* the hair on the nape has a wide blackish base, for instance in the holotype specimen BM 78.7.3.4, while in *L. europaeus* the basal fringe is short and grey, for example in specimen USNM 153400.

C) **Rump** (Fig. 7, 3). — In *L. europaeus* there is a conspicuous patch of grey over the rump in winter pelage. This patch is due to the mixed effect of the subterminal and terminal rings of the dominant hair which are white and black, respectively. *L. corsicanus* does not have this conspicuous patch because the subterminal ring of the dominant hair over the rump does not turn to white in winter as in *L. europaeus*. On the contrary, it remains nearly the same color as the rest of the dominant hair of the dorsal pelage.

In *L. corsicanus* the rump color is normally somewhat lighter than the back as in other hare species but this is because the terminal and medial bands of the dominant hair and the upper band of the underfur have less black or are not so dark in the rump region as in the center of the back where they are intensely black. Specimens AMNH 190956, AMNH 160959 of *L. corsicanus* in winter pelage display an almost uniform back with a rump hardly distinguishable by the change of color from the rest of the upper parts while specimen MF 11586 belonging to *L. europaeus* displays a noticeable grey patch on the rump.

D) **Facial bands** (Fig. 7, 4). — *L. corsicanus* usually shows a greyish white facial band on both sides of the head in winter pelage, extending from the preocular patch to the lower base of the ears, over the lower cheeks. Specimens MNHN 1919-670, MF 11592, BM 78.7.3.4, BM 8.9.30.1, BM 98.2.9.1, BM 98.2.9.2 are normal representatives of this character. These facial bands are not present in most specimens of *L. europaeus*. In the Italian sample only specimen MF 11586 with strongly marked winter pelage as revealed by the conspicuous grey patch on the rump has a kind of facial band but not as extensive and with the same pattern as in *L. corsicanus*.

E) **Subocular patches** (Fig. 7, 5). — The Corsican hare displays a conspicuous ochraceous-tawny patch extending underneath and behind the eye which is more obvious in winter pelage because of the marked contrast with the white facial patch; it is not present in *L. europaeus*. This character was already noticed by de Winton (1898) as one of the peculiarities of *L. corsicanus*. Specimens BM 8.9.30.1 and MNHN 1919-670 of *L. corsicanus* are very representative as regards this character. A smaller patch of the same color is also present in the whisker area of *L. corsicanus*.

F) **Collar** (Fig. 7, 6). — The collar is very uniform in color in the two species, having a marked vinaceous tonality in *L. europaeus* which varies between light vinaceous cinnamon and cinnamon-buff, and a marked buff tonality in *L. corsicanus*, which varies from pinkish buff to cinnamon-buff. Representative specimens are MF 10874, MF 11593, MF 11594 of *L. europaeus* and BM 98.2.9.1, BM 13.1.900, BM 78.7.3.4 of *L. corsicanus*.

G) **Inner surface of forelimbs** (Fig. 7, 7). — In *L. corsicanus* there is a well-marked light buff area in the inner side of the forelimb contrasting with the clay color of the outer surface, while in *L. europaeus* the inner buff area is less marked and the color of the forelimb is almost uniform clay-sorrel.

H) **White hair extension in underparts** (Fig. 7, 8). — The area of white pelage on the underparts is more extensive in *L. corsicanus* than in *L. europaeus*, basically because *L. corsicanus* lacks the transitional fringe between dorsal and ventral pelage that is typical in *L. europaeus*. Specimens BM 78.7.3.4, BM 8.9.30.1, BM 98.2.9.1, BM 98.2.9.2, MF 10870, MF 11592 are representative examples of *L. corsicanus*.

I) **Transitional pelage between back and belly** (Fig. 7, 9). — In *L. europaeus* there is always a transitional fringe on the sides separating the dorsal and ventral pelage. It is very uniform in color, varying between light vinaceous cinnamon and vinaceous cinnamon. In *L. europaeus* specimen USNM 153400 this character is very well represented. As stated previously, *L. corsicanus* lacks this band and presents a marked contrast between the dorsal and ventral pelage. Specimens quoted in the previous section are also typical examples of this character in *L. corsicanus*.

## Geographic distribution

Fig. 9 shows the geographic localities appertaining to all the studied specimens for *L. europaeus* and *L. corsicanus*. The localities of *L. europaeus* show that up to the end of the 19th century this species occupied the northern part of the Italian Penin-

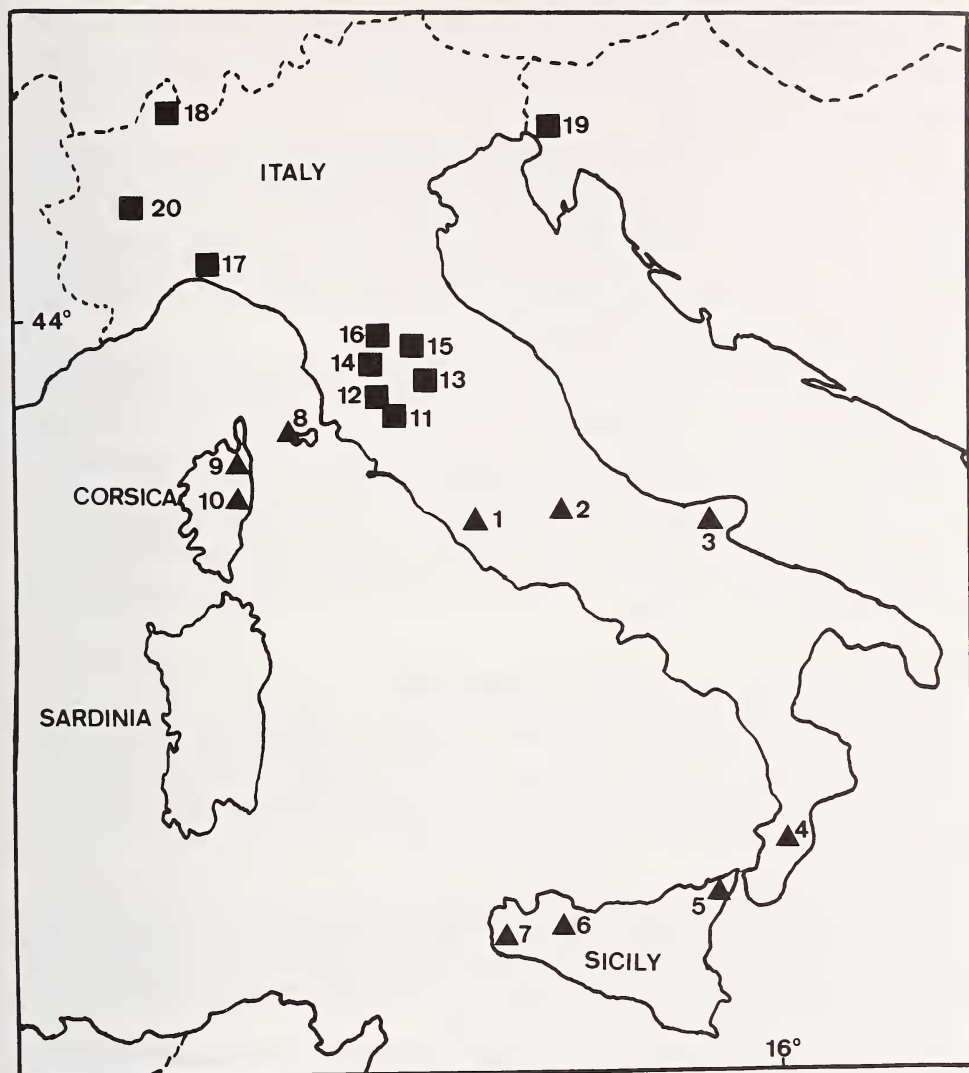


Fig. 9: Evidence on the pattern of distribution of indigenous hares in Italy based on localities of museum specimens. Localities of *L. europaeus* (black squares) correspond to specimens collected in the 19th century, and localities of *L. corsicanus* (black triangles) correspond to all the available specimens in collections, some of them belonging to this century. 1 — surroundings of Rome, 2 — Lago Fucino, 3 — Monti di Gargano, Foggia, 4 — Mongiana, 5 — Saponara, 6 — Vicari, 7 — Marsala, 8 — Isola d'Elba, 9 — Bastia, 10 — Aleria, 11 — San Casciano di Bagni, 12 — Siena, 13 — Arezzo (Alpe de la Luna), 14 — Gabbiano, Camugliano, Bientina, 15 — Rassina, 16 — Maiano, Firenze (Florence), 17 — Genova, 18 — Domodossola, 19 — Trieste, 20 — Torino (Turin).

sula and the localities of *L. corsicanus* indicate that this species occupied the southern part of the Italian Peninsula, Sicily, Corsica and Elba Island.

It is likely that this parapatric pattern corresponds to the natural distribution of the species, with probably a contact zone existing between Siena and Rome. These localities are the most southerly and the most northerly points, respectively, of *L. europaeus* and *L. corsicanus*.

The Corsican hare appears to be originally from the southern part of the Italian Peninsula where this species probably was geographically confined after the expansion of *L. europaeus* throughout Europe. The distribution of *L. corsicanus* in Sicily could be the result of introduced hares as is the case in Corsica where, according to Vigne (1988), hares were released no later than in the 16th century. This could also be the case of Elba Island from where the only known specimens are to be found in the Museum La Specola in Florence (MF).

Current *L. europaeus* distribution in Italy does not conform to the natural situation because of artificial introductions carried out throughout Italy from the beginning of the 20th century. The present distribution of *L. corsicanus* in Italy is not well known and this species could be in frank regression as a result of hunting and habitat reduction by *L. europaeus* introduced from other European countries. The capture of two *L. corsicanus* specimens in Catanzaro in 1974 and 1975 (INBS collection) suggests that this species could still exist in some mountainous parts of southern Italy. In Corsica, Vigne (1988) reports the decline of *L. corsicanus*, also due to hunting and the introduction of *L. europaeus*.

#### Phenetic relationships amongst SW European hares

To assess the phenetic relationships existing among *L. corsicanus*, *L. europaeus*, *L. castroviejoi* and *L. granatensis* a stepwise discriminant analysis using the 29 skull variables was carried out. The *L. europaeus* and *L. corsicanus* specimens are those from Italy. The *L. granatensis* specimens were caught in Palencia and Cádiz provinces while the *L. castroviejoi* specimens were caught in Palencia, León and Asturias provinces, all in Spain.

The analysis was checked to determine if the groups were different. The MANOVA test shows an F value of 33.42 ( $P < 0.0001$ ) which means that the differences among groups are very significant. Missing values were estimated and included in a analysis after making a stepwise estimation within species which provides a value for each variable case using only the correlated variables.

The analysis was able to produce a discriminant function with 5 of the 29 variables (MMPH, DFZ, TBW, WSP, and TL). The classification matrix indicates that 100 % of the specimens were classified correctly into the groups according to the classification function. However, the jackknife classification matrix indicates that 97.6 % of

Table 9: F values computed from the Mahalanobis  $D^2$  statistics that test the equality of group means for each pair of groups in the stepwise discriminant analysis based on skull size variables. Group means are plotted in Fig. 10.

	<i>L. corsicanus</i>	<i>L. europaeus</i>	<i>L. castroviejoi</i>
<i>L. europaeus</i>	56.02		
<i>L. castroviejoi</i>	14.97	45.31	
<i>L. granatensis</i>	34.98	29.93	42.74



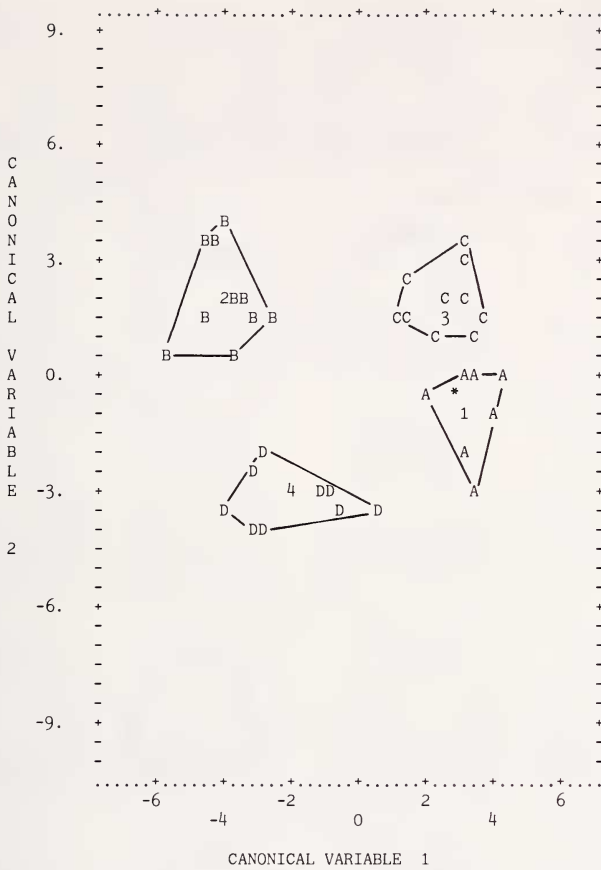


Fig. 10: Scatter plot for the first two canonical variables of the stepwise discriminant analysis carried out using skull variables of SW European hares. Group A represents specimens of *L. corsicanus*, B of *L. europaeus*, C of *L. castroviejoii*, and D of *L. granatensis*. 1, 2, 3, and 4 are the group means on which the test of equality showed in Table 9 is based.

the specimens were classified correctly into the groups, 100 % of *L. europaeus*, *L. castroviejoii* and *L. granatensis*, and 90 % of *L. corsicanus*, because one specimen of this species was mistaken for *L. castroviejoii*.

Dispersion scattergrams for the first two canonical variables of the discriminant-function analysis (Fig. 10) showed no overlapping in the phenotypes of the four species. The total variance explained by the first two canonical variables was 90.8 %. Canonical variable 1 explains 61.6 % of the variance and separates *L. corsicanus* and *L. castroviejoii* from *L. europaeus* and *L. granatensis*. Canonical variable 2 explains 29.2 % of the variance and separates *L. granatensis* and *L. corsicanus* from *L. castroviejoii* and *L. europaeus*.

Table 9 shows the test of equality of group means for each pair of groups. *L. europaeus*—*L. corsicanus* are the most differentiated species with a value of 56.02.

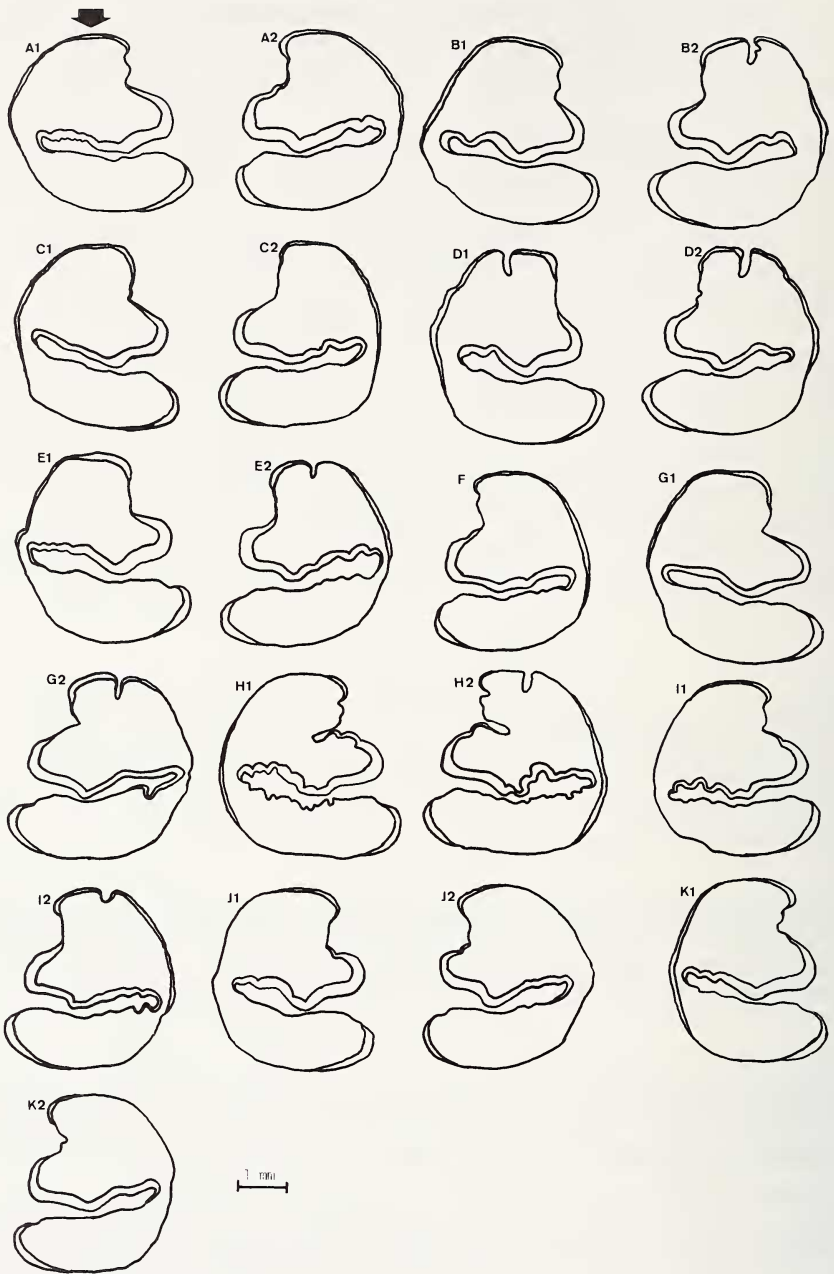


Fig. 11: Camera lucida drawings of occlusal sections of P/3 of several adult specimens of *L. castroviejoi*. A1 and A2 — UZA 1983.10.24.02 (right and left), B1 and B2 — UZA 1983.10.28.01, C1 and C2 — UZA 1983.10.28.02, D1 and D2 — UZA 1983.10.28.03, E1 and E2 — UZA 1983.11.16.01, F — UZA 1983.11.16.03 (left), G1 and G2 — UZA 1983.11.19.01, H1 and H2 — UZA C2/86, I1 and I2 — UZA C3/86, J1 and J2 — UZA C4/86, K1 and K2 — UZA C5/86.

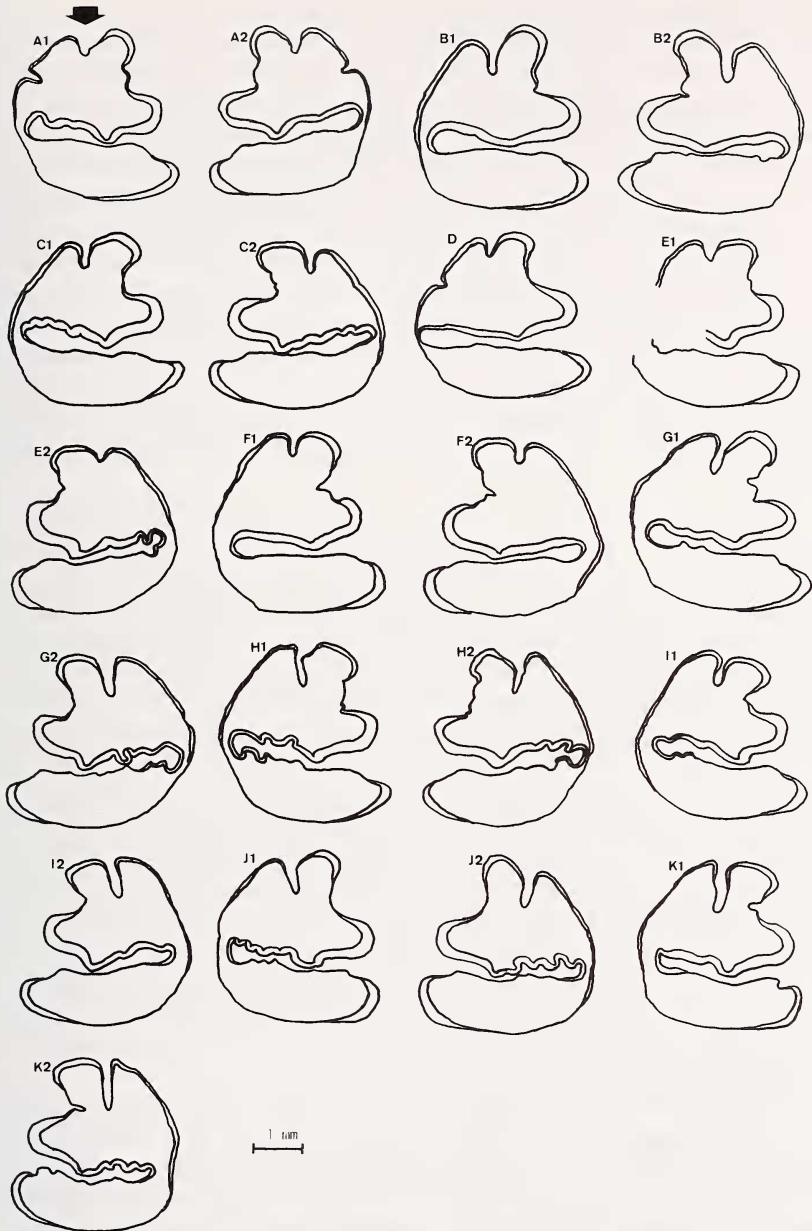


Fig. 12: Camera lucida drawings of occlusal sections of P/3 of different adult specimens of *L. corsicanus*. A1 and A2 — BM 19.7.7.2341, B1 and B2 — BM 98.2.9.1, C1 and C2 — BM 78.7.3.4, D — BM 8.9.30.1 (right), E1 and E2 — MZ 10870, F1 and F2 — MZ 10871, G1 and G2 — MZ 11526, H1 and H2 — MZ 11588, I1 and I2 — INBS 3830, J1 and J2 — AMNH 160956, K1 and K2 — AMNH 160959.

This distance is near that existing between *L. europaeus*—*L. castroviejo* (45.31) and *L. castroviejo*—*L. granatensis* (42.74). The least differentiated species according to the selected variables are the pairs *L. corsicanus*—*L. granatensis* (34.98), *L. europaeus*—*L. granatensis* (29.93), and *L. castroviejo*—*L. corsicanus* (14.97). Thus, this last pair shows the biggest phenetic similarity according to the analysis. The affinity between *L. corsicanus* and *L. castroviejo* is supported by other kinds of information such as skull morphology and pelage color and pattern. However, they show some important morphologic differences, particularly as regards the enamel structure of P/3 where *L. castroviejo* shows unique characters within the context of the genus *Lepus* and *L. corsicanus* resembles the other European species. Fig. 11 and 12 show different P/3 drawings of *L. castroviejo* and *L. corsicanus* corresponding to adult specimens in which the lack or extreme smallness of the anteroflexid in *L. castroviejo* is noteworthy in comparison with the regular *Lepus* anteroflexids of *L. corsicanus*. It is also noteworthy that in P2/ *L. castroviejo* usually has a very slight mesoflexus while *L. corsicanus* normally has a well-defined mesoflexus as in Fig. 5, a.

### Discussion

All the comparative analyses made in this paper provide clear evidence of the marked phenetic differentiation between *L. europaeus* and *L. corsicanus* in Italy. A number of discriminant variables and characters exist which, without exception, separate all the specimens of each species. The maximum distinctiveness between the two species was found comparing the skull size, cranial characters, and pelage color and pattern. Therefore, the indigenous hares of Italy previously identified as *L. europaeus* are here considered to be two different species (*L. europaeus* and *L. corsicanus*).

Each species is very homogeneous morphologically. The phenetic characteristics of all the specimens of *L. corsicanus* from Corsica, Elba Island, the southern Italian Peninsula, and Sicily fully correspond to those of the holotype from Corsica which belongs to an introduced population. In the case of *L. europaeus* there is no phenetic difference between the old specimens studied in this paper and specimens recently collected in Italy, originating mostly from restocking with hares from other European countries. This finding is also supported by comparison with some brown hare specimens indigenous to other countries around Italy (Switzerland, Croatia, France, Spain) studied in different collections.

Phenetic distinction within other pairs of hare species from SW Europe has been based on similar characters (Palacios 1989). In the case of *L. europaeus* and *L. granatensis* these characters are external measurements, skull size and pelage pattern, and in the case of *L. europaeus* and *L. castroviejo* they are mainly pelage pattern and dental morphology. In these cases geographic patterns of distribution were also parapatric (Palacios & Meijide 1979), except for the pair *L. europaeus* and *L. castroviejo* which, having a basically parapatric pattern may also show a reduced local sympatry (Bonhomme et al. 1986). Natural geographic hare distribution patterns in Europe are now altered. This situation also affects Spain where, over the last 20 years, artificial introductions of *L. granatensis* have been made in the area of *L. europaeus*.



Biochemical characters have also been very useful to distinguish among Spanish hares (Palacios 1979, Bonhomme et al. 1986) but this kind of results is not yet available for the comparison of Italian hares.

As regards the taxonomic relationships among SW European hares resulting from the stepwise discriminant analysis based on skull measurements, the four species appear well-differentiated. *L. castroviejo* and *L. corsicanus* are the closest but they differ significantly in some skull variables such as DFZ, TL, ENL, IFL and TBL which are smaller in *L. corsicanus*. Moreover, there are also differences in pelage color and in dental characters which are considered relevant to lagomorph phylogeny, particularly those related to the anteroflexid in P/3. On the basis of these differences I consider that it is most appropriate to maintain the species validity of *L. corsicanus* and *L. castroviejo* pending further morphological, biochemical and molecular work.

The enamel pattern in *L. corsicanus* dentition in Italy is uniform, for instance the anteroflexid in P/3 is large in all localities, including those from Corsica, Elba Island, and Sicily and is never slight or absent as it is in *L. castroviejo*. So it is difficult to support the view that *L. corsicanus* is the result of an old introduction of *L. castroviejo* specimens, or vice versa, because the dental states present in this species do not exist in *L. corsicanus*. Data from Sicily do not support the idea of hare introduction by the Greeks in the fifth century BC in the terms mentioned by Corbet (1986) because there are no *L. europaeus* specimens from Sicily in collections. If the Greeks had carried out any artificial introduction in Sicily, it could have been with *L. corsicanus* specimens captured on the southern Italian mainland. However, in the current state of knowledge it is difficult to make any hypotheses regarding the presence of *L. corsicanus* in Sicily because it could have reached the island by natural means.

The present areas of *L. castroviejo* and *L. corsicanus* seem residual. On the base of their phenetic similarity it could be hypothesized that these species probably had a common ancestor occupying a large distribution area in SW Europe before the expansion of *L. europaeus*. The paleontological material should be studied again in the light of the characters currently available permitting the species distinction, particularly those related to tooth morphology, in order to provide new light on the zoogeography and evolution of this group.

*L. corsicanus* is a taxon which requires revalidation as a valid species and must be added to the catalog of living mammals of the Italian Peninsula. Old World hare taxonomy is currently very confused and *L. corsicanus* was not the only example of this situation. Therefore, a great research effort to clarify the systematics of this group should be made, considering that species like *L. corsicanus* may be disguised locally and need identifying because they may be in danger of extinction.

I recommend surveying the *L. corsicanus* population in Italy and undertaking a species protection plan in the areas where this hare is still living because it seems likely that this species could be threatened at present due to intense hunting and restocking with brown hares throughout the whole of its distribution area. I hope that these comments stimulate sufficient interest in Italy and France to ensure that conservation measures and actions to save this interesting hare will be undertaken soon.

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### Zusammenfassung

Hasen von der italienischen Halbinsel und Sizilien werden üblicherweise einer einzigen Art (*Lepus europaeus* Pallas, 1778) zugeordnet. Eine taxonomische Untersuchung, basierend auf Größe, Morphologie und Fellmerkmalen autochthoner Exemplare aus Museumssammlungen, ergibt dagegen, daß sie zwei verschiedenen Arten zugehören (*L. europaeus* und *L. corsicanus* de Winton, 1898). Die Kartierung der Fundorte beider Hasen zeigt, daß sie natürlicherweise parapatrische Areale einnahmen, *L. europaeus* im Norden und *L. corsicanus* im Süden Italiens, mit einer Trennungslinie zwischen Sienna und Rom. Beide Arten sind phänetisch klar getrennt, ihre Unterscheidung ist mit Hilfe univariater und multivariater Statistiken möglich. Die phänetischen Charakteristika jeder Art in ihrem natürlichen Verbreitungsgebiet sind bemerkenswert gleichförmig. Zwischenformen wurden nicht gefunden; Exemplare aus benachbarten Orten weisen keine intermediäre Eigenschaften auf. Bei den Unterscheidungsmerkmalen, die diese beiden Arten voneinander trennen, spielt die Farbe des Rückenunterfells adulter Exemplare eine besondere Rolle, die bei *L. europaeus* immer weiß und bei *L. corsicanus* grau ist. Die Schädelgrößen unterscheiden sich in einigen Abmessungen, wobei *L. corsicanus* kleiner ist als *L. europaeus*. Ein wichtiges Zahnmerkmal ist die posteriore Kontur im Querschnitt des ersten oberen Schneidezahns, der bei *L. europaeus* konkav, bei *L. corsicanus* konvex ist. Statistische Vergleiche der Schädel- und Zahnmerkmale weisen hohe Chiquadratwerte und sehr geringe Ähnlichkeiten auf, was auf einen deutlichen Unterschied zwischen beiden Arten schließen läßt. *L. corsicanus* zeigt im Vergleich mit anderen SW-europäischen Hasen die größte phänetische Ähnlichkeit mit *L. castroviejo* und die geringste mit *L. europaeus*. Die Ergebnisse lassen vermuten, daß *L. corsicanus* und *L. castroviejo* einen gemeinsamen Vorfahren hatten, der vor der Ausbreitung von *L. europaeus* ein großes Verbreitungsgebiet in SW-Europa zwischen Italien und Spanien einnahm.

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#### Appendix 1: *L. corsicanus* material examined

##### Istituto Nazionale di Biologia della Selvaggina, Bologna (INBS)

- 3306 Mongiana, Catanzaro, Italy, 18 Apr 1975, mounted skin, skull inside, female, juvenile.  
3830 Mongiana, Catanzaro, Italy, Oct 1974, skin and skull, age III.

##### Museo Zoologico de “La Specola”, Firenze (MF)

- 10870 Saponara, Milazzo, Sicily, 3 Dec 1883, mounted skin, skull, male, age IV.  
10871 Vicari, Palermo, Sicily, 12 Dec 1883, mounted skin, skull, female, age IV.  
11526 Aleria, Corsica, 3 Oct 1889, mounted skin, skull, male, age IV.  
11588 Isola d'Elba, Italy, 25 Feb 1877, mounted skin, skull, male, age IV.  
11590 Isola d'Elba, Italy, 12 Feb 1877, mounted skin, skull inside, female, adult.  
11592 Foggia, Italy, 21 Feb 1908, mounted skin, skull inside, male, adult.

##### Muséum National d'Histoire Naturelle, Paris (MNHN)

- 1894-37 Corsica, mounted skin, adult.  
1919-670 Bastia, Corsica, mounted skin, adult.  
1962-2546 Corsica, 29 Sept 1910, skull, age II.

**Natural History Museum, London (BM)**

- 8.9.30.1 Surroundings of Rome, Italy, 13 Jan 1900, skin and skull, male, age IV.  
 19.7.7.2341 Corsica, Nov 1883, skull, age IV.  
 78.7.3.4 Bastia, Corsica, Jan 1875, skin and skull, male, age IV, Holotype.  
 98.2.9.1 Marsala, Sicily, Jan 1898, skin and skull, male, age IV.  
 98.2.9.2 Marsala, Sicily, Jan 1898, skin and skull, age III.

**American Museum of Natural History (AMNH)**

- 160956 Abruzzo, Lago Fucino, Italy, Dec 1935, skull, female, age IV.  
 160959 Monti del Gargano, Vieste, Puglia, Foggia, Italy, Dec 1933, skull, female, age IV.

**Appendix 2: *L. europaeus* material examined****Museo Zoologico "La Specola", Firenze (MF)**

- 10871 (dupl) This skull has been extracted from the mounted *L. corsicanus* skin n. 10871 and belongs to *L. europaeus*. As the true skull of the specimen n. 10871 was already prepared in collection, I have included the *L. europaeus* skull in the study with the number 10871 (dupl), assuming that it could have a similar date to 10871 (around 1883) and could be a local specimen (probably of the surroundings of Florence). It seems likely that the *L. europaeus* skull was used to facilitate the mounting of the specimen n. 10871. The skull n. 10871 (dupl) corresponds to relative age IV.
- 10872 Alpe della Luna, Arezzo, Italy, 9 Nov 1885. This specimen consists of a mounted skin of *L. europaeus* with skull inside, and another skull which is prepared in collection and also belongs to *L. europaeus*. As both the mounted skin and the prepared skull have the same label data, it is likely that the mounted skin and the skull inside do not belong to the same specimen, it being possible that this second skull was used for naturalization only. Male specimen. Both the mounted skin and the prepared skull correspond to age IV.
- 10873 S. Casciano di Bagni, Siena, Italy, 10 Jan 1900, skull only, male, age III.  
 10874 Rassina, Arezzo, Italy, 31 Jan 1890, mounted skin, prepared skull, male, age IV.  
 11523 Maiano, Firenze, Italy, 18 Sept 1899, skull only, male, age III.  
 11524 S. Casciano di Bagni, Siena, Italy, 10 Jan 1900, skull only, female, age III.  
 11525 Gabbiano, Greve, Firenze, Italy, 23 Dec 1899, skull only, male, age IV.  
 11527 Surroundings of Trieste, Italy, Jan 1889, skull only, age IV.  
 11584 Alpi di Domodossola, Italy, Sept 1876, mounted skin, skull inside, male, juvenile.  
 11585 Camugliano, Toscana, Italy, 2 Nov 1880, mounted skin, skull inside, male, adult.  
 11586 Torino, Italy, 10 Dec 1883, mounted skin, skull inside, male, adult.  
 11587 Greve, Firenze, Italy, 20 Aug 1900, mounted skin. It is written on the label that this specimen has a detached skull but it is not in collection. Examining the skin it seems that the skull is not inside either. Female, juvenile.
- 11591 S. Maria a Monte, Bientina, Italy, 20 Sept 1883, mounted skin, skull inside, female, adult.  
 11594 Firenze, Italy, Jan 1873, mounted skin, skull inside, female, adult.  
 11595 Firenze, Toscana, Italy, Oct 1838, mounted skin, skull inside, male, adult.  
 11596 Firenze, Toscana, Italy, Dec 1837, mounted skin, skull inside, male, adult.  
 11597 Domodossola, Italy, June 1887, skull only, age III.  
 11598 Domodossola, Italy, June 1887, skull only, age III.  
 11599 Domodossola, Italy, June 1887, skull only, age II.

**Natural History Museum London (BM)**

- 19.7.7.2486 Genova, Italy, Feb 1884, skull only, age IV.  
 98.10.2.18 Surroundings of Siena, Italy, 2 Feb 1898, skin and skull, male, age IV.  
 98.10.2.19 Siena, Italy, 13 March 1898, skin and skull, male, age IV.

**National Museum of Natural History (USNM)**

- 153399 Siena, Italy, 29 Dec 1898, skin and skull, female, age III.  
 153400 Siena, Italy, 15 Nov 1898, skin and skull, female, age IV.



**Appendix 3: Alphabetical list of abbreviations of body and skull measurements****a) Body**

E	Ear length
HB	Head and body length
HF	Hindfoot length
T	Tail length

**b) Skull**

ANW	Anterior nasal width, taken between the prominences of the nasal processes of the incisive bones.
DPFP	Diameter of the posterior foramen palatinum.
DFZ	Diameter of foramen zygomaticus.
DIRSIM	Distance between the incisor root and sutura incisivomaxillaris.
ENL	External nasal length
FIL	Foramen incisivum length.
FIW	Foramina incisiva width.
FTL	Facial tubercle length.
FUISL	First upper incisor section length.
FUISW	First upper incisor section width.
HPMM	Height of processus muscularis mandibulae, taken between the anterior margin of processus articularis and the tip of the process, perpendicular to the margin.
INL	Internal nasal length.
LCTRL	Lower cheek-tooth row length.
MH	Mandible height.
MLCP	Mandible length, taken from the capitulum.
NPB	Narrowing of the palatine bridge.
PL	Palatal length.
PNW	Posterior nasal width.
PPW	Postpalatal width.
PZW	Posterior zygomatic width.
RIC	Radius of the first upper incisor curvature.
RW	Rostral width.
SFW	Smallest frontal width.
TBL	Tympanic bulla length.
TBW	Tympanic bulla width.
TL	Total length.
UCTRL	Upper cheek-tooth row length.
WFT	Width between facial tubercles.
WSP	Width between supraorbital processes.